Austral ECOLOGY A Journal of ecology in the Southern Hemisphere

Austral Ecology (2013) **38**, 289–299

Meta-analysis of the effects of small mammal disturbances on species diversity, richness and plant biomass

MEREDITH ROOT-BERNSTEIN* AND LUIS A. EBENSPERGER
CASEB and Departamento de Ecología, Facultad de Ciencias Biológicas, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile (Email: mrootbernstein@bio.puc.cl)

Abstract The disturbance activities of many small mammals, including building burrows, mounds, trails and tunnels, and herbivory, can have significant impacts on their ecosystems, both through trophic and non-trophic interactions. Some species have large enough impacts through their disturbances to be classed as ecosystem engineers and/or keystone species. Others have negative or null effects. However, at present it is difficult to predict whether the disturbances created by a given species will have significant effects on common measures of ecosystem response such as species richness, diversity and biomass. We ask whether variables characterizing disturbance type, responding species, disturbance-making species and the environment can predict changes in magnitude and direction of effects on biomass, richness and diversity. We test these predictions with a meta-analysis of 106 data entries in a database derived from 63 papers, representing 40 small mammal species. We find that small mammal disturbances in general increase biomass, and both increase and decrease richness and diversity. We also identify individual environmental, disturbance-related, and species-related variables associated with these changes in magnitude and direction. We discuss the likely interactions between these variables, and how current proxy measures of disturbance impact could be replaced by more accurate direct measures. We recommend that future studies focus on conditions characterized by combinations of variables we identify as significant, in order to understand how these variable interactions (which cannot be analysed through meta-analysis) affect disturbance outcomes. Based on the gaps in our database and results, we also recommend that future studies directly measure disturbance impact, measure disturbance effects on animal and well as plant taxa, and take measurements on multiple scales.

Key words: biomass, disturbance, diversity, mammal, meta-analysis, richness.

INTRODUCTION

Many small fossorial and semi-fossorial mammals create disturbances through the building of burrows, mounds, underground tunnels and above-ground trails, herbivory, and combinations of these activities (Huntly 1991; Jones *et al*. 1997; Wilby *et al*. 2001). Some disturbance-creating species have been identified as keystone species, defined as species with disproportionate contributions to ecosystem functioning primarily through trophic interactions (Mills *et al*. 1993; Jordán *et al*. 2009) (plateau pikas (Smith & Foggin 1999; Lai & Smith 2003); pairie dogs (Miller *et al*. 2000; Davidson & Lightfoot 2006); kangaroo rats (Brock & Kelt 2004; Davidson & Lightfoot 2006) and European rabbits (Delibes-Mateos *et al*. 2008)). Several small mammals have also been described as ecosystem engineers (prairie dogs (Alba-Lynn & Detling 2008; Davidson *et al*. 2008); kangaroo rats (Davidson *et al*. 2008); European rabbits (Gálvez-Bravo *et al*. 2009); pocket gophers (Reichmann & Seabloom 2002); and plateau zokors (Zhang *et al*. 2003)), meaning species whose activities physically produce, through non-trophic interactions, altered habitat used by themselves or other taxa (Jones *et al*. 1994).

Both keystone species and ecosystem engineers are reported to have strong positive effects on measures such as species diversity, richness and biomass (e.g. Davidson & Lightfoot 2006; Gálvez-Bravo *et al*. 2009). By contrast, many studied small mammal disturbances are reported to have no effect, or negative effects, on species diversity, richness and biomass (e.g. Mallory & Heffernan 1987; Zenuto & Busch 1995; Rogers *et al*. 2001; Semenov *et al*. 2001). We are still unable to identify the critical factors that predict whether a small mammal species will be a keystone species and/or an ecosystem engineer, or have negative or null effects, because of its disturbance activities. As disturbance effects of many small mammal species, particularly those in the southern hemisphere, remain insufficiently studied, an opportunity exists to improve theory and predict *a priori* the magnitude and direction of effects on other species of their disturbance activities. This could facilitate the development of

---

*Corresponding author.

Accepted for publication April 2012.

doi:10.1111/j.1442-9993.2012.02403.x

small mammals as natural habitat restoration tools (Dhillion 1999; Eldridge & James 2009).

Disturbance by biological agents is considered to be a driver of plant and animal diversity and richness at intermediate temporal and spatial scales, although the evidence is mixed (Connell 1961; Mackey & Currie 2001). According to the intermediate disturbance theory, a certain level of disturbance prevents dominant competitors from competitively excluding other species, thus increasing community richness and diversity (Shea *et al.* 2004). Competition between species may also be limited through endogenous disturbances or 'perturbations' such as predation and herbivory (Proulx & Mazumder 1998). Competition between species is expected to be dependent on variables such as disturbance impact (i.e. how 'intermediate' it is relative to the species competition parameters), and climate, soil and habitat characteristics (Shea *et al.* 2004). Disturbance 'intermediacy' or impact in turn is expected to depend on differences in disturbance intensity, frequency, duration and scale (Olff & Ritchie 1998; Whitford & Kay 1999; Whittaker *et al.* 2001; Kerley *et al.* 2004; Shea *et al.* 2004; Wright 2009). Responding taxa (including animals) may be differentially sensitive to different disturbance regimes (Jones *et al.* 1997; Kerley *et al.* 2004; Shea *et al.* 2004; Tews *et al.* 2004). Environmental factors such as climate conditions and community types are also expected to play roles in determining the strength of different taxa's responses to small mammal disturbances (Olff & Ritchie 1998; Whitford & Kay 1999; Kerley *et al.* 2004; Wright 2009), by altering interspecific competition (Shea *et al.* 2004). Productivity, which is also affected by these environmental factors, is expected to increase the tolerance of communities to disturbance (Shea *et al.* 2004), and is associated with highest richness at intermediate values (Proulx & Mazumder 1998). Thus, environmental and abiotic factors are expected to influence responses to small mammal disturbances in at least three interacting, non-independent ways: through interspecific competition, through differing responses to disturbance, and by affecting productivity.

Ecosystem engineering provides an alternative, if not entirely independent, framework for thinking about small mammal disturbances. Ecosystem engineering may either increase or decrease plant and animal diversity and abundance (Jones *et al.* 1994; Wright & Jones 2004; Hastings *et al.* 2007). Increases are expected to occur if the ecosystem engineering creates habitat heterogeneity, leading to open niche opportunities (Tews *et al.* 2004; Wright & Jones 2004). Wright and Jones (2004) show that across ecosystem engineering studies, primarily of small mammal disturbances, increases in productivity, measured as biomass, predict increases in species richness. Parameters such as the identity of the engineering species, the nature or intensity of the disturbance, or the species composing the responding community seem to have only an 'idiosyncratic' relationship to the species richness response (Wright & Jones 2004). However, Wright and Jones' (2004) study did not examine whether any of these parameters can predict variation in biomass.

Though conceptually elegant, these hypotheses are not very helpful in predicting which species in what habitats will have positive, negative or null effects on richness, diversity and biomass through their disturbance activities. The Wright and Jones (2004) ecosystem engineering model of disturbances does not explain under what conditions biomass increases because of disturbance activities, and the intermediate disturbance hypothesis largely depends on *a posteriori* identification of 'intermediate' disturbances (Shea *et al.* 2004).

We addressed some of these theoretical shortcomings using meta-analytic tools. First, we asked whether variables characterizing disturbances, affected species and affected habitats predict changes in biomass. Second, we avoided the theoretically useful but practically unwieldy definition of 'intermediate' disturbance and simply asked whether these variables also predict changes in biomass, richness and diversity. Our database consisted of studies reporting species (plant and animal) richness, species (plant and animal) diversity, and plant biomass. We asked whether these measures show a significant change (either upwards or downwards) in the presence or high density, compared with absence or low density, of disturbance-creating small mammals. Next, we considered whether differences in effect direction and magnitude of species richness, diversity or biomass can be predicted by measures of disturbance type and impact, climate, habitat and responding taxa. We were able to assemble a database larger those used by previous analyses (Proulx & Mazumder 1998; Shea *et al.* 2004; Wright & Jones 2004). The overall size, however, was constrained by the fact that studies of small mammal disturbances report a wide variety of effects, not always including changes in species richness, diversity or biomass, and report several different indices of disturbance.

At a more proximate level, our study was intended to explain why some species disturbances have negative effects on species diversity, richness and biomass, and others have positive effects. At a more ultimate level, our study aimed to identify study systems that merit further research effort in order to clarify key variable interactions that can be incorporated by theoretical approaches, to state predictions about the effects of currently unstudied small mammal disturbances, and to stimulate the study of small mammals as habitat restoration agents.

METHODS

Data set

Studies were compiled in 2010 and 2012 from an existing collection of papers on this topic previously collected by one of us (LE), by following up references in the texts of papers, and by searches in Web of Science and Google Scholar. Searching in 2010 had two phases. First we searched in Web of Science and Google Scholar for reports of mammals of body mass up to 6 kg that created trails, runways, mounds, burrows, tunnels or lawns. Although 6 kg is arguably medium-sized, this cut-off allowed us to include important relevant research on European rabbits, vizcachas, and marmots, which with woodchucks were the only species above 1 kg included in our database. Based on the species identified during this phase, we conducted searches in Web of Science and Google Scholar using the terms 'richness', 'diversity' and 'biomass' combined with the scientific species names of all species identified in the previous phase. In 2012 we further searched the complete archives of *Journal of Mammalogy* for reports of mammals less than 6 kg that make trails, runways, mounds, burrows, tunnels or lawns. Based on this species list we searched in Google Scholar for each species binomial in combination with the terms 'richness', 'diversity' and 'biomass'. We considered richness to refer to measures of total taxa number of animals or plants (usually species, sometimes morphospecies), and diversity to refer to a measure incorporating both evenness and richness, that is, Shannon's diversity index (Purvis & Hector 2000). We only included in our database studies that met two criteria: (i) they reported diversity, richness, and/or biomass in any taxon, including animals and plants; and (ii) they compared (or incidentally reported a comparison between) sites with low density or absence of the focal small mammal species and its disturbances, and sites with high density or the presence of the focal species and its disturbances. We considered these to be the minimum requirements needed to assess and compare the impact of any kind of small mammal disturbance on any taxa across studies. In one case we excluded a paper because, after corresponding with the author, it was not clear that the plots in habitat where the species occurred included their disturbances. Three articles divided plants responding to disturbance into life form categories different from the most common categories (i.e. invasive and native plants rather than forbs, grasses, herbs or shrubs). We were not able to include these studies because there were few of them, and their results were not comparable to the majority of studies. Two papers were discarded because they reported Simpson's instead of Shannon's diversity index. After this process of study collection we had 89 studies in our database. Of the 89 studies meeting our selection criteria, some had to be discarded because of statistical problems. Two studies were excluded because of apparent problems of pseudoreplication. A further total of 31 studies did not report critical statistics needed to compute effect size (e.g. t-values, F-values, d.f., or N). Of these, five studies were kept in the database upon obtaining this information from their authors. Further seven studies were included by using raw data reported in the publication to redo the statistical tests and generate the unreported effect sizes. The remaining 19 were discarded. Five studies used statistical tests that we could not find information on how to convert to Fisher's z transform (see below). Ultimately 63 studies were considered in the meta-analysis. Forty species of small mammal from 13 families and three orders (Diprotodotia, Lagomorpha, Rodentia) were represented in the database (Table 1).

Whenever studies reported multiple results, for example, if the effects on arthropods and plants were reported separately, these were treated as distinct entries in our database. Similarly, results for different years reported separately were treated as individual entries. However, whenever results for multiple overlapping spatial scales were reported, only one was entered in the database. The final database consisted of 106 entries from 63 papers: 66 results for effects on richness, 44 results for effects on diversity, and 19 results for effects on plant biomass. The complete database is included in the Appendix S1.

Some limitations inherent to the database need to be highlighted. Statistically, the number of entries included in the study may seem relatively small. However, this number is within the range of recent meta-analyses conducted on similar topics (Mackey & Currie 2001; Shea *et al.* 2004). The number of small mammal species included is less than the number of small mammal species that make disturbances, and tropical or subtropical species are under-represented. These limitations in part reflect that many published studies concerning the disturbances made by small mammal species do not meet the two criteria listed above for study selection. In other cases, studies were excluded as they were descriptive, not focused on the responses of other taxa to disturbances reported, or measured a related but not comparable response variable, such as individual species abundances (population sizes), plant damage, seed banks, community composition, or nesting success. In spite of these caveats, we do not expect our analysis to suffer overly from the file-drawer problem, in which nonsignificant or negative results are not published. Of the entries included in the meta-analysis, 36 (34%) reported negative effect sizes, and 22 (21%) reported no effects. Fail-safe numbers are a straightforward way to assess the seriousness of the file-drawer effect (Rosenberg 2005). The fail-safe numbers reported in the results section show the number of additional nonsignificant results expected to be needed to significantly change the results.

Predictor variables

We collected three classes of variables: (i) species attributes, including disturbance characteristics; (ii) study site characteristics; and (iii) variables related to how or what data were measured (Table 1). The terms selected for categorical variables were derived from those used in the included studies, and consequently are not necessarily all at the same level of description (e.g. reptiles and grasses are not phylogenetic groups at equivalent scales). This reflects inconsistency in what is measured and how study characteristics are reported across studies, which we did not attempt to correct for.

For variables related to species and their disturbances, we looked for a measure of the impact of disturbance (Olff & Ritchie 1998). However, we were unable to find a common measure of disturbance impact across studies used in the

doi:10.1111/j.1442-9993.2012.02403.x

Table 1. Variable names, categories used and their sources consulted for the meta-analysis

Variable	Variable categories	Source
Small mammal characteristics		
Species	Various; Diprotodotia: Potoroidae: *Bettongia lesueur* Rodentia: Chinchillidae: *Lagostomus maximus* Cricetidae: *Microtus arvalis; M. cabrerae; M. dudecimcostatus; M. ochrogaster; M. oeconomus; M. californicus; M. pennsylvanicus; Lemmus lemmus; Ondatra zibethicus* Ctenomidae: *Ctenomys australis; C. mendocinus* Geomyidae: *Geomyidae spp.; Geomys bursarius; G. attwateri; G. pinetis; Thomomys mazama; T. bottae; T. talpoides* Heteromyidae: *Dipodomys spectabilis; D. ingens* Hystricidae: *Hystrix indica* Muridae: *Tatera brantsii* Octodontidae: *Octodon degus; Spalocopus cyanus* Sciuridae, Marmotini: *Cynomys ludovicianus; C. gunnisoni; C. ludovicianus* & *harvester ants; C. spp.* & *Dipodomys spectabilis; Marmota camtschatica bungei; M. monax; M. sibirica; Spermophilus parryii* Spalacidae: *Myospalax fontanierii* Lagomorpha: Leporidae: *Oryctolagus cuniculus* Ochotonidae: *Ochotona curzoniae; O. curzoniae* & *Alticola stoliczkanus* [Rodentia, Cricetidae]; *O. pallasi; O. princeps*	Articles in database (see Appendix S1)
Disturbance type	Burrow; burrow & lawn; herbivory; mound; mound & herbivory; mound & runway; runway	Articles in database
Fossoriality	Fossorial; semi-fossorial	Articles in database
Sociality	Group-living; solitary	http://animaldiversity.ummz.umich.edu
Body mass	Continuous variable	http://genomics.senescence.info/species/; Pembleton and Williams (1978); Korn (1987); Williams and Cameron (1991); Williams and Kilburn (1991); Arthur *et al.* (2008)
Lifespan	Continuous variable	http://genomics.senescence.info/species/; Pembleton and Williams (1978); Korn (1987); Williams and Cameron (1991); Williams and Kilburn (1991)
Study site characteristics		
Biogeographical region	Alpine; arctic; Mediterranean; semi-arid; subarctic; temperate	Articles in database
Habitat type	Grassland; grassland/shrubland; montado; steppe; temperate forest; tundra/taiga	Articles in database
Precipitation	Continuous variable	Articles in database
Soil fertility	Fertile; infertile	Articles in database; NRCS (1999)
Data characteristics		
Study scale	Between; within	Articles in database
Taxon measured	Birds; forbs; forbs & grasses; grasses; herptiles; invertebrates; mammals; perennial plants; plants (general)	Articles in database

For the variable 'species', families and orders are shown for reference but were not used as variables. For further descriptions of how studies were categorized see *Methods*.

meta-analysis. Instead, we recorded the small mammal species or combination of species in the study, the type of disturbance(s) considered, and other species characteristics (Table 1).

Habitat and climate, including soil and precipitation conditions, are considered important factors in determining the strength of responses to small mammal disturbances (Olff & Ritchie 1998; Whitford & Kay 1999; Kerley *et al.* 2004; Wright 2009). Consequently, our variables related to study site characteristics included biogeographic region, habitat type, average yearly precipitation or precipitation for the year of the study, and soil fertility (Table 1). We took these data from the articles in the database. Habitat type was not independently classified; we used whatever term was used in the article. When precipitation data were not recorded we looked up local weather records for the study site, or other published descriptions of the same site. To estimate soil fertility we noted the soil type described and consulted two soil taxonomy guides (NRCS 1999; Chesworth 2008). When soil type was not recorded, we looked up the probable soil type on maps available from the United States Department of Agriculture (http://soils.usda.gov/use/worldsoils/mapindex/Global_Soil_Orders_Map.jpg, accessed 2010). We considered mollisols, ultisols, vertisols, alfisols and andisols to be fertile, and others to be infertile. For 19 cases in which we could not determine the kind of soil at the study site we classified soil fertility as 'unknown'.

For variables related to data characteristics we recorded the taxonomic group in which responses to small mammal disturbances were measured, as different species may respond differently to the same disturbances (Tews *et al.* 2004). Only one study measured a response in lichens, which we classed as plants. We also classed studies as measuring effects at one of two scales: 'within' or 'between'. Studies at the 'within' scale compared sites on or next to disturbances with sites at a fixed, small distance (on a scale of metres) from disturbances. Studies at the 'between' scale compared randomly located sites within an area affected by small mammal disturbances to sites in another area unaffected by small mammal disturbances. Table 1 summarizes all variables and categories used in the meta-analysis.

Data analysis

The statistical treatment followed Rosenberg *et al.* (2000), and the analysis was conducted in MetaWin (Rosenberg *et al.* 2000). We calculated the correlation coefficient r for each entry in the database, which we then converted into Fisher's z transform, a universal measure of effect size (Rosenberg *et al.* 2000). For studies in which only the significance (*P*) value was reported, we converted *P*-value ranges to z following Rosenthal and DiMatteo (2001). We also calculated the asymptotic variance of z which we used to weight effect sizes in the meta-analysis (Rosenberg *et al.* 2000). We chose to use a random effects model because we were interested in extrapolating the effects of the treatments beyond the database, and assumed that random variation exists between studies (Petitti 1994; Rosenberg *et al.* 2000). Results for richness, diversity and biomass were treated as separate meta-analyses. Although diversity incorporates data on richness, two areas with equal richness can have different diversities, and vice versa (Purvis & Hector 2000), so we considered the two measures to be effectively independent. Biomass and richness can be related but we considered these two response variables to be independent for the following reasons. Wright and Jones (2004) reported a functional relationship between high biomass and high plant species richness, but did not show whether this relationship holds for low biomass or for plant biomass and non-plant richness. Additionally, the relationship between plant biomass and plant richness has been reported to be non-linear (Oba *et al.* 2001; Bhattarai *et al.* 2004). For these two reasons, we assume that biomass and richness are effectively independent. The summary effect sizes were calculated in MetaWin (Rosenberg *et al.* 2000).

We first considered the absolute values of z to ask whether small mammal disturbances had strong or weak effects, independent of direction. This is a methodological innovation which is able to detect cases in which a given variable predicts both negative and positive effect sizes (Schechter 1997). This is likely to be the case where the variable in question is not the variable directly controlling effect direction (Pearl 2000). A significant result for the absolute value of effect sizes indicates a probable indirect interaction between the variable in question and some other variable, while a significant result for a signed value indicates a direct influence on the effect size and direction (Pearl 2000). This can be explained with a hypothetical example: if rabbits have a significant positive effect on richness, we attribute the increase in richness to the variable 'rabbits'. If rabbits have a significant effect on the *absolute value* of richness effect sizes this means we see strong positive and strong negative effect sizes. This could be because rabbits allow plant communities to invade which are species-rich in some cases, but species-poor in other cases; thus 'rabbits' has an effect apparently mediated by an interaction with the variable 'plant community'.

In addition to looking at absolute values of effect sizes, we ran the analyses again for the signed values of z to ask whether effects were negative or positive. It should be noted that inverting some of the data across the *y*-axis (giving it back its negative sign) changed the shape of the data distribution, making the two analyses non-pseudoreplicated (Fig. 1). Alpha was set at 0.05 for both absolute and signed effect size analyses. We also reported the Q statistic, which is a measure of variation across z scores in the studies, and the fail-safe number, which is an estimate of the number of additional results with effect size of zero that would need to be added to significantly reduce the observed mean effect size (Rosenthal 2001), both of which are calculated by MetaWin. Continuous variables were assessed with Pearson's correlation coefficient in the program R.

RESULTS

Signed effect sizes, overall analysis

Impacts on richness, diversity and biomass were a mix of both positive (increases) and negative (decreases). Signed effect sizes were not different from zero for richness and diversity. For richness, the mean effect size was 0.09 ($P > 0.05$, d.f. = 65, 95% CI =

doi:10.1111/j.1442-9993.2012.02403.x

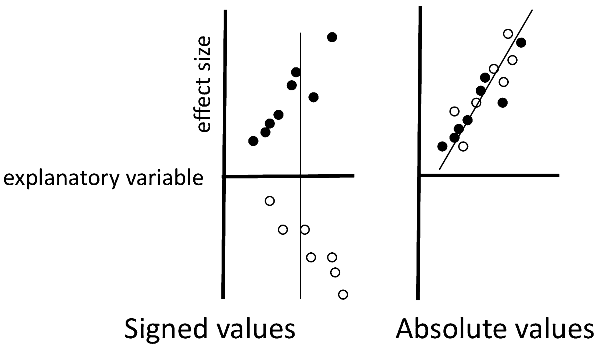

Fig. 1. Visual representation of signed and absolute values of effect sizes. This illustrative figure shows how absolute values of effect sizes can be interpreted. In many cases in our data, small mammals show both strong negative and strong positive effect sizes (figure on the left), and consequently the best fit line did not have a slope significantly different from zero. However, in absolute value the negative effect sizes are reflected over the *x*-axis (figure on the right), and then the data often show a significant relationship to the explanatory variable in question, indicating that effect strength, but not direction, is influenced by the variable.

–0.0192–0.1977; Q = 390.9, fail-safe number = 54.1). For diversity, the mean effect size was –0.03 ($P > 0.05$, d.f. = 43, 95% CI = –0.7111–0.6468; Q = 17.8, fail-safe number = 0.0). There was a significant effect size for biomass of 0.92 ($P < 0.05$, d.f. = 11, 95% CI = 0.0566–1.7778; Q = 14.1, fail-safe number = 17.8).

Absolute value effect sizes, overall analysis

We found statistically significant large impacts (both negative and positive) on richness, diversity and biomass as a result of small mammal disturbances. Effect sizes linked to richness, diversity and biomass were all significantly different from zero. For richness, the mean effect size is 0.68 ($P < 0.05$, d.f. = 65, 95% CI = 0.5684–0.7829; Q = 243.57, fail-safe number = 3907.6, Rosenthal's method). For diversity, the mean effect size is 1.01 ($P < 0.05$, d.f. = 43, 95% CI = 0.3821–1.6373; Q = 10.36, fail-safe number = 126.9, Rosenthal's method). For biomass, the mean effect size is 1.38 ($P < 0.05$, d.f. = 17, 95% CI = 0.9065 to 1.85; Q = 19.2, fail-safe number = 246.3, Rosenthal's method).

Independent variables

Because of the large number of variables and analyses, we report only significant results. These results are summarized in Tables 2 and 3. Overall, we found large positive effect sizes for many variables on biomass, both smaller positive and large negative effects of several variables on richness, but no variables predicting signed effect sizes for diversity. As shown in Table 2, the majority of the largest positive effects were biomass effects, caused by habitat type (grassland), biogeographic region (semi-arid), study scale (within), type of disturbance (burrows), body mass (increasing), fossoriality (semi-fossorial), sociality (group-living), precipitation (increasing), and small mammal lifespan (increasing). Richness was increased by *Lagostomus maximus*, type of disturbance (herbivory, burrows, burrows and lawns), study scale (between), habitat type (grassland/shrubland, grassland), biogeographic region (alpine, semi-arid), and semi-fossoriality. Richness was decreased by type of disturbance (mounds), habitat type (steppe), biogeographic region (subarctic, subtropical), and *Marmota camtschatica*. No variables predicted the direction of changes in diversity. As shown in Table 3, the largest absolute value effects were again mostly biomass effects, caused by sociality (solitary), type of disturbance (mounds), soil (infertile), fossoriality (fossorial), taxon measured (plants), and habitat type (grassland/shrubland). Relatively smaller effects on diversity were found for the variables type of disturbance (mounds), soil (fertile), taxon measured (plants), sociality (group-living), fossoriality (semi-fossorial), body mass (increasing), lifespan (increasing), study scale (within), and precipitation (increasing). In general, the smallest magnitude absolute value effects were for richness effects, produced by biogeographic region (temperate and Mediterranean), fossoriality (semi-fossorial), soil fertility (fertile, infertile, unknown), sociality (group-living, solitary), taxon measured (plants), body mass (increasing), lifespan (increasing), precipitation (increasing), study scale (within), *Oryctolagus cuniculus* and *Cynomys ludovicianus*.

DISCUSSION

General findings

We found large and generally positive effects of small mammal disturbances on plant biomass. In contrast, the effects of small mammals on richness and diversity of species were more variable (negative and positive), relatively smaller, and low fail-safe numbers indicate that a small number of potentially unpublished non-significant results would alter the findings for effect direction (but not magnitude). Our analysis suggests that these patterns are contingent upon several factors. Specifically, biomass of plants showed large effect sizes under the influence of variables characterizing habitat, climate, disturbance characteristics, and life history attributes of the disturbance-making small mammal species. If variables interact linearly, biomass should be highest as precipitation increases in semi-arid grasslands disturbed by larger, longer-lived group-living semi-fossorial burrow-making species. By contrast, richness and diversity of species overall showed both

doi:10.1111/j.1442-9993.2012.02403.x

Table 2. Analyses of signed effect sizes

Variable name	Variable value	Explains . . .	Effect size	d.f.	95% CI
Small mammal species	*L. maximus*	Richness	**2.15**	2	1.2001–3.0978
Habitat type	Grassland	Biomass	**2.08**	4	0.1749–3.9794
Biogeographic region	Semi-arid	Biomass	**1.60**	8	0.7231–2.4742
Study scale	Within	Biomass	**1.29**	10	0.0831–2.4888
Type of disturbance	Burrows	Biomass	**1.26**	5	0.1878–2.3338
Type of disturbance	Herbivory	Richness	**1.20**	7	0.8311–1.5856
Body mass	Increasing	Biomass	**1.18**	14	0.4719–1.8908
Fossoriality	Semi-fossorial	Biomass	**1.09**	9	0.1051–2.0695
Sociality	Group living	Biomass	**0.99**	9	0.0560–1.9174
Precipitation	Increasing	Biomass	**0.91**	17	0.0757–1.7533
Lifespan	Increasing	Biomass	**0.87**	16	0.0054–1.7408
Study scale	Between	Richness	**0.62**	20	0.4168–0.8423
Habitat type	Grassland/shrubland	Richness	**0.58**	13	0.3447–0.8140
Biogeographic region	Alpine	Richness	**0.56**	6	0.1768–0.9467
Type of disturbance	Burrows	Richness	**0.36**	12	0.1007–0.6228
Biogeographic region	Semi-arid	Richness	**0.32**	28	0.1814–0.4582
Type of disturbance	Burrows and lawns	Richness	**0.30**	12	0.0603–0.5396
Habitat type	Grassland	Richness	**0.29**	32	0.1585–0.4274
Fossoriality	Fossorial	Richness	**0.18**	50	0.0486–0.3017
Type of disturbance	Mounds	Richness	**–0.42**	26	–0.5676—0.2592
Habitat type	Steppe	Richness	**–1.01**	8	–1.2720—0.7421
Biogeographic region	Subarctic	Richness	**–1.22**	6	–1.5140—0.9265
Small mammal species	*M. camtschatica*	Richness	**–1.42**	5	–1.7164—1.1202
Biogeographic region	Subtropical	Richness	**–1.53**	2	–2.6256—0.4356

All effect sizes are significant ($P < 0.05$). Variable combinations are listed in order of effect size. Note the negative effect sizes at the bottom of the table.

strong negative and strong positive responses to small mammal disturbances. Richness was both moderately increased and strongly decreased by different values of variables characterizing biogeographical region, habitat type, disturbance type and small mammal species identity. Richness should be highest in shrubland–grassland habitats in alpine or semi-arid regions disturbed by species that make burrows and lawns. Richness should be lowest in subarctic steppes disturbed by mound-builders, or in subtropical regions. By contrast, there were no variables that controlled the direction of diversity effects. The magnitude of diversity effects was affected by variables related to species life history attributes, soil fertility, responding taxa and study scale.

As hypothesized and demonstrated by others, productivity-related variables are likely to release species from interspecific competition and nutrient limitation at intermediate values, allowing biomass, richness and diversity to increase (Proulx & Mazumder 1998; Mackey & Currie 2001; Shea *et al.* 2004; Michalet *et al.* 2006). However, our results suggest that additional factors interact to limit observed increases in biomass, richness and diversity to a subset of small mammal disturbance conditions. We conceive of different types of variables as acting as filters on possible outcomes (Fig. 2). Below we describe the likely interactions between these variables.

We hypothesize that behavioural and life history characteristics of small mammal species such as sociality, extent of fossorial habits, body size and lifespan would influence factors such as the density, scale and duration of disturbances. These disturbance impacts should interact to influence richness, diversity and biomass of plants and other species (Jones *et al.* 1997; Olff & Ritchie 1998; Whitford & Kay 1999; Kerley *et al.* 2004; Wright 2009). Specifically, herbivory and the creation of lawns in association with burrows may affect interspecific competition more strongly than the opening of physical spaces for colonization and seedling recruitment (Louda *et al.* 1990; Hobbs & Huenneke 1992; Keane & Crawley 2002; Otfinowski & Kenkel 2010). Biogeographical conditions influence the distribution of small mammal species and disturbance-responding species over communities. Biogeography may thus influence the incidence of ruderal and grazing-adapted plants, or heterogeneity-tolerant animals that may exploit disturbances (Holmgren *et al.* 2000; Ricklefs & Bermingham 2002; Devictor & Robert 2009). Transitions between community types may also be especially easy to facilitate through disturbance in grass and grass/shrub communities (Brown & Heske 1990; Wesche *et al.* 2007; Acácio *et al.* 2009). Given the disturbance characteristics and the species pool, species responses to disturbance and the observed hump-shaped

Table 3. Analyses of absolute value of effect sizes

Variable name	Variable value	Explains . . .	Effect size	d.f.	95% CI
Habitat type	Forest	Richness	**1.54**	3	1.0144–2.0795
Sociality	Solitary	Biomass	**1.49**	6	0.4852–2.4938
Type of disturbance	Mounds	Biomass	**1.44**	4	0.4585–2.4280
Soil	Infertile	Biomass	**1.35**	10	0.6970–2.0094
Fossoriality	Fossorial	Biomass	**1.32**	7	0.4887–2.1560
Taxon measured	Plants	Biomass	**1.23**	13	0.7868–1.6648
Type of disturbance	Mounds	Diversity	**1.17**	18	0.1645–2.1708
Soil	Fertile	Diversity	**1.17**	29	0.3971–1.9530
Habitat type	Grassland/shrubland	Biomass	**1.15**	11	0.5191–1.7801
Biogeographic region	Temperate	Richness	**1.08**	2	0.3067–1.8476
Taxon measured	Plants	Diversity	**1.08**	33	0.3561–1.8002
Sociality	Group-living	Diversity	**1.07**	22	0.1635–1.9728
Fossoriality	Semi-fossorial	Diversity	**1.04**	31	0.2840–1.7869
Body mass	Increasing	Diversity	**1.03**	41	0.3755–1.6832
Lifespan	Increasing	Diversity	**1.03**	41	0.3750–1.6838
Study scale	Within	Diversity	**1.01**	29	0.2343–1.7762
Precipitation	Increasing	Diversity	**1.01**	43	0.3686–1.6508
Fossoriality	Semi-fossorial	Richness	**0.78**	50	0.6545–0.9041
Soil fertility	Fertile	Richness	**0.73**	19	0.5306–0.9323
Sociality	Group-living	Richness	**0.73**	40	0.6016–0.8737
Soil	Infertile	Richness	**0.71**	33	0.5578–0.8532
Taxon measured	Plants	Richness	**0.71**	42	0.5843–0.8400
Body mass	Increasing	Richness	**0.66**	65	0.5739–0.7467
Lifespan	Increasing	Richness	**0.66**	65	0.5733–0.7548
Precipitation	Increasing	Richness	**0.66**	64	0.5488–0.7637
Study scale	Within	Richness	**0.64**	44	0.5107–0.7602
Sociality	Solitary	Richness	**0.57**	24	0.3907–0.7503
Small mammal species	*O. cuniculus*	Richness	**0.54**	4	0.1186–0.9576
Small mammal species	*C. ludovicianus*	Richness	**0.53**	7	0.2256–0.8364
Soil fertility	Unknown	Richness	**0.48**	11	0.2078–0.7601
Biogeographic region	Mediterranean	Richness	**0.40**	9	0.1606–0.6382

All effect sizes are significant ($P < 0.05$). Variable combinations are listed in order of effect size. The table excludes variable combinations that were also significant for signed effect sizes ($n = 24$) because this information is redundant (see Table 2). The table presents only the variable combinations that were not significant for signed effect sizes.

competition–productivity relationship will determine what species are present at a given time in the course of disturbance creation (Proulx & Mazumder 1998; Mackey & Currie 2001; Shea *et al.* 2004; Tews *et al.* 2004; Michalet *et al.* 2006). If measurements of disturbance effects cross community types with different responses to the same disturbance, effects may be amplified or confused.

Directions for future research

Many small mammal species disturbance effects on species diversity, richness and biomass remain to be studied. Based on the data set used on this study, it is clear that small mammals from Africa and Australia are particularly under-represented. These include, but are not limited to, elephant shrews (Rathbun & Rathbun 2006), porcupines (Dean & Milton 1991), Cape ground squirrels, meerkats (Waterman & Roth 2007), woylies (Claridge & May 1994; Garkaklis *et al.* 2003, 2004), whistling rats (Jackson 2000), and mole rats (Whitford & Kay 1999). Effects of trails or runways were under-represented in our database compared with burrows and mounds. Studies measuring richness and diversity of non-plant taxa were also under-represented.

Further research in this area should address several questions that were raised by our meta-analysis, or which we were not able to adequately address because of insufficient published data. (i) The identity of variables that control directionality of effects on diversity should be investigated, assuming that such variables exist but have not been identified by this meta-analysis. Comparative studies of same species across biogeographic regions or habitats (e.g. European rabbits in the European Mediterranean, South America and Australia; Iriarte *et al.* 1989; Eldridge & Simpson 2002; Delibes-Mateos *et al.* 2008) and of interactions between species with different disturbance types (Wilby *et al.* 2001; Bagchi *et al.* 2006; Davidson & Lightfoot 2006, 2007) could help to identify these variables. (ii) By identifying sets of variables from Table 2 that may reasonably be expected to co-occur and interact, we can look for test cases where strong negative or positive

doi:10.1111/j.1442-9993.2012.02403.x

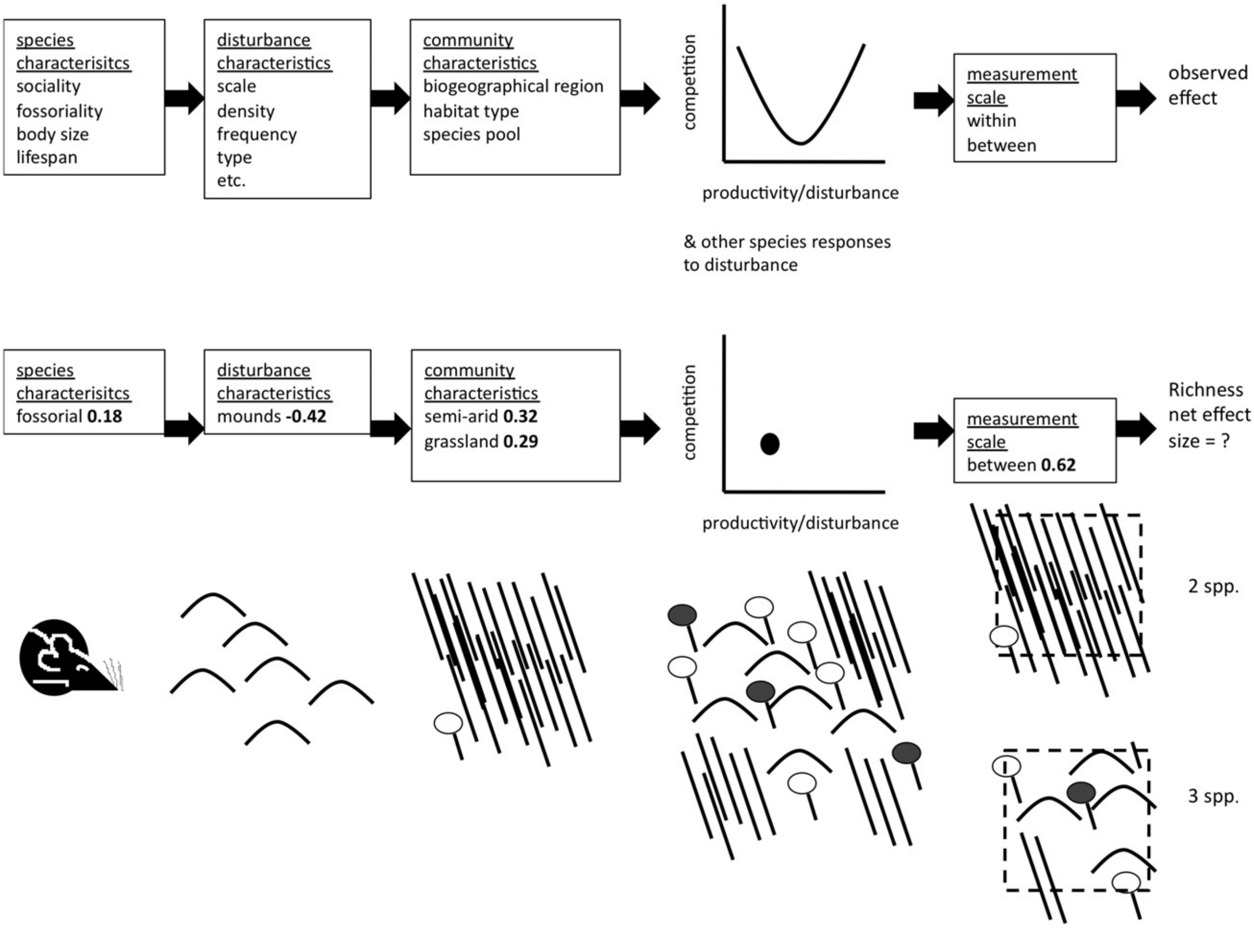

Fig. 2. Above, an illustration of how sets of variables may filter the conditions under which the humped productivity–competition relationship results in an effect on richness, diversity or biomass. The black arrows indicate interactions between sets of variables. Neither these interactions, nor interactions between variables in each set, are currently well understood. In the second row, a hypothetical example for effects on plant richness. Effect sizes listed after variables are taken from the Results. As interactions between variables are unknown, we cannot calculate an expected net effect size in this scenario. In the third row, a visual illustration of the hypothetical example in the second row. At far left, a rodent in a hole. Second from left, mounds. Third from left, grasses and a flowering forb. Second from right, grasses, two types of flower, and mounds.

effects on species richness are predicted. These may include mound-building subtropical species (negative effects), or lawn-forming species in semi-arid grasslands (positive effects). (iii) Similarly, we can identify from Table 3 species under a combination of variables expected to have both negative and positive effects on a particular response variable. For instance, small-bodied semi-fossorial group-living species in Mediterranean habitat regions should have a moderate mixed effect on richness. Further study of these variable combinations may allow us to understand how these variables interact, or whether other variables interact with them to give the overall effect size and direction. (iv) As Wright and Jones (2004) showed that high biomass and high richness are related, but did not test the inverse, special attention should be given to variable combinations where we may expect high richness but low biomass. For example, small bodied, short-lived solitary fossorial species that make mounds in shrublands (Tables 2,3). (v) We have identified a shortfall of studies measuring responses by non-plant taxa, yet different taxa may respond to disturbances in different ways (Tews *et al.* 2004). Field studies following these suggestions may help to clarify the theoretical understanding of community responses to small mammal disturbance, and could lead to applications of small mammals as habitat restoration agents (Dhillion 1999; Eldridge & James 2009).

We also hope that future meta-analyses and reviews on this topic will be able to include an improved range of studies and variables. This can be achieved partly by adopting experimental approaches and measurement techniques that will facilitate comparison of results across species and sites. These include (i) measuring and reporting effects on biomass, richness and diversity; (ii) the use of multiple common measures of disturbance impact; and (iii) the use of sampling

doi:10.1111/j.1442-9993.2012.02403.x

designs which incorporate both 'within' and 'between' scales. According to our results, effect size direction for species richness is dependent on the scale at which effects are measured. Adopting these practices should improve our understanding of small mammal disturbance effects.

ACKNOWLEDGEMENTS

Many thanks to Eileen Lacy and two anonymous referees for helpful comments which improved the manuscript, and to L. Galvez Bravo, W. Wesche, D. Eldridge, C. Alba-Lynn, R. Zenuto, and D. Kelt for providing additional data and information about their studies. MR-B was supported by a graduate fellowship from CONICYT (No. 63105446). Funding was provided by CASEB (Program 1) and FONDECYT grant #1090302 to LAE.

REFERENCES

Acácio V., Holmgren M., Rego F., Moreira F. & Mohren G. M. (2009) Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? *Agrofor. Syst*. **76,** 389–400.

Alba-Lynn C. & Detling J. K. (2008) Interactive disturbance effects of two disparate ecosystem engineers in North American shortgrass steppe. *Oecologia* **157,** 269–78.

Arthur A. D., Pech R. P., Davey C., Jiebu, Yanming Z. & Hui L. (2008) Livestock grazing, plateau pikas and the conservation of avian biodiversity on the Tibetan plateau. *Biol. Conserv.* **141,** 1972–81.

Bagchi S., Namgail T. & Ritchie M. E. (2006) Small mammalian herbivores as mediators of plant community dynamics in the high-altitude arid rangelands of Trans-Himalaya. *Biol. Conserv.* **127,** 438–42.

Bhattarai K. R., Vetaas O. R. & Grytnes J. A. (2004) Relationship between plant species richness and biomass in an arid subalpine grassland of the central Himalayas. *Nepal. Folia Geobot.* **39,** 57–71.

Brock R. E. & Kelt D. A. (2004) Keystone effects of the endangered Stephen's kangaroo rat (*Dipodomys stephensi*). *Biol. Conserv.* **116,** 131–9.

Brown J. H. & Heske E. J. (1990) Control of a desert-grassland transition by a keystone rodent guild. *Science* **250,** 1705–7.

Chesworth W., ed. (2008) *Encyclopedia of Soil Science*. Springer, Dordrecht.

Claridge A. W. & May T. W. (1994) Mycophagy among Australian mammals. *Aust. J. Ecol.* **19,** 251–75.

Connell J. H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle Chthamalus stellatus. *Ecology* **4,** 710–23.

Davidson A. D. & Lightfoot D. C. (2006) Keystone rodent interactions: prairie dogs and kangaroo rats structure the biotic composition of a desertified grassland. *Ecography* **29,** 755–65.

Davidson D. A. & Lightfoot D. C. (2007) Interactive effects of keystone rodents on the structure of desert grassland arthropod communities. *Ecography* **30,** 515–25.

Davidson D. A., Lightfoot D. C. & McIntyre J. L. (2008) Engineering rodents create key habitat for lizards. *J. Arid Environ.* **72,** 2142–9.

Dean W. R. J. & Milton S. J. (1991) Disturbances in semi-arid shrubland and arid grassland in the Karoo, South Africa: mammal diggings as germination sites. *Afr. J. Ecol.* **29,** 11–16.

Delibes-Mateos M., Delibes M., Ferreras P. & Villafuerte R. (2008) Key role of European rabbits in the conservation of the Western Mediterranean Basin hotspot. *Conserv. Biol.* **22,** 1106–17.

Devictor V. & Robert A. (2009) Measuring community responses to large-scale disturbance in conservation biogeography. *Divers. Distrib.* **15,** 122–30.

Dhillion S. S. (1999) Environmental heterogeneity, animal disturbances, microsite characteristics, and seedling establishment in a *Quercus havardii* community. *Restoration Ecol.* **7,** 399–406.

Eldridge D. J. & James A. I. (2009) Soil-disturbance by native animals plays a critical role in maintaining healthy Australian landscapes. *Ecol. Manage. Restor.* **10** S27–34.

Eldridge D. J. & Simpson R. (2002) Rabbit (*Oryctolagus cuniculus L.*) impacts on vegetation and soils, and implications for management of wooded rangelands. *Basic Appl. Ecol.* **3,** 19–29.

Gálvez-Bravo L., Belliure J. & Rebollo S. (2009) European rabbits as ecosystem engineers: warrens increase lizard density and diversity. *Biodivers. Conserv.* **18,** 869–85.

Garkaklis M. J., Bradley J. S. & Wooler R. D. (2003) The relationship between animal foraging and nutrient patchiness in south-west Australian woodland soils. *Aust. J. Soil Res.* **41,** 665–73.

Garkaklis M. J., Bradley J. S. & Wooler R. D. (2004) Digging and soil turnover by a mycophagous marsupial. *J. Arid Environ.* **56,** 569–78.

Hastings A., Byers J. E., Crooks J. A. *et al*. (2007) Ecosystem engineering in space and time. *Ecol. Lett.* **10,** 153–64.

Hobbs R. J. & Huenneke L. F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conserv. Biol.* **6,** 324–37.

Holmgren M., Avilés R., Sierralta L., Segura A. M. & Fuentes E. R. (2000) Why have European herbs so successfully invaded the Chilean matorral? Effects of herbivory, soil nutrients, and fire. *J. Arid Environ.* **44,** 197–211.

Huntly N. (1991) Herbivores and the dynamics of communities and ecosystems. *Annu. Rev. Ecol. Syst.* **22,** 477–503.

Iriarte J. A., Contreras L. C. & Jaksic F. M. (1989) A long-term study of a small-mammal assemblage in the central Chilean matorral. *J. Mamm.* **70,** 79–87.

Jackson T. P. (2000) Adaptation to living in an open arid environment: lessons from the burrow structure of the two southern African whistling rats, *Parotyomys brantsii* and *P. littledalei*. *J. Arid Environ.* **46,** 345–55.

Jones C. G., Lawton J. H. & Shachak M. (1994) Organisms as ecosystem engineers. *Oikos* **69,** 373–86.

Jones C. G., Lawton J. H. & Shackak M. (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78,** 1946–57.

Jordán F., Lui W. & Mike A. (2009) Trophic field overlap: a new approach to quantify keystone species. *Ecol. Model.* **220,** 2899–907.

Keane R. M. & Crawley M. J. (2002) Exotic plant invasions and the enemy release hypothesis. *TREE* **17,** 164–70.

Kerley G. I. H., Whitford W. G. & Kay F. R. (2004) Effects of pocket gophers on desert soils and vegetation. *J. Arid Environ.* **58,** 155–66.

Korn H. (1987) Densities and biomasses of non-fossorial southern African savanna rodents during the dry season. *Oecologia* **72,** 410–13.

doi:10.1111/j.1442-9993.2012.02403.x

Lai C. H. & Smith A. T. (2003) Keystone status of plateau pikas (*Ochotona curzoniae*): biodiversity of native birds. *Biodivers. Conserv.* **12,** 1901–12.

Louda S. M., Keeler K. H. & Holt R. D. (1990) Herbivore influence on plant performance and competitive interactions. In: *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman) pp. 413–44. Academic Press, New York.

Mackey R. L. & Currie D. J. (2001) The diversity-disturbance relationship: is it generally strong and peaked? *Ecology* **82,** 3479–92.

Mallory F. F. & Heffernan T. D. (1987) Floristic modification of low Arctic tundra by the Arctic ground squirrel, Spermophilus parryi. *Canad. Field Nat.* **101,** 388–99.

Michalet R., Brooker R.W., Cavieres L. A. *et al.* (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecol. Lett.* **9,** 767–73.

Miller B., Reading R., Hoogland J. *et al.* (2000) The role of prairie dogs as keystone species: response to Stapp. *Conserv. Biol.* **14,** 318–21.

Mills L. S., Soulé M. E. & Doak D. F. (1993) The keystone-species concept in ecology and conservation. *Bioscience* **43,** 219–24.

NRCS (1999) *Soil Taxonomy: A Basic System of Soil Classification for Making and Interpreting Soil Surveys*. USDA, Washington.

Oba G., Vetaas O. R. & Stenseth N. C. (2001) Relationships between biomass and plant species richness in arid-zone grazing lands. *J. App. Ecol.* **38,** 836–45.

Olff H. & Ritchie M. E. (1998) Effects of herbivores on grassland plant diversity. *TREE* **13,** 261–5.

Otfinowski R. & Kenkel N. C. (2010) Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. *Biol. Invasions* **12,** 1349–61.

Pearl J. (2000) *Causality: Models, Reasoning and Inference*. Cambridge University Press, Cambridge.

Pembleton E. F. & Williams S. L. (1978) Geomys pinetis. *Mamm. Species* **86,** 1–3.

Petitti D. B. (1994) *Meta-Analysis, Decision Analysis, and Cost-Effectiveness Analysis: Methods for Quantitative Synthesis in Medicine*. OUP, Oxford.

Proulx M. & Mazumder A. (1998) Reversal of grazing impact on plant species in nutrient-poor vs. nutrient-rich ecosystems. *Ecology* **79,** 2581–92.

Purvis A. & Hector A. (2000) Getting the measure of biodiversity. *Nature* **405,** 212–19.

Rathbun G. B. & Rathbun C. D. (2006) Social structure of the bushveld sengi (*Elephantulus intufi*) in Namibia and the evolution of monogamy in the Macroscelidea. *J. Zool.* **269,** 391–9.

Reichmann O. J. & Seabloom E. W. (2002) The role of pocket gophers as subterranean ecosystem engineers. *TREE* **17,** 44–9.

Ricklefs R. E. & Bermingham E. (2002) The concept of the taxon cycle in biogeography. *Global Ecol. Biogeogr.* **11,** 353–61.

Rogers W. E., Hartnett D. C. & Elder B. (2001) Effects of plains pocket gopher (*Geomys bursarius*) disturbances on tallgrass prairie structure. *Am. Midl. Nat.* **145,** 344–57.

Rosenberg M. S. (2005) The file-drawer problem revisited: a general weighted method for calculating fail-safe numbers in meta-analysis. *Evolution* **59,** 464–8.

Rosenberg M. S., Adams D. C. & Gurevich J. (2000) *MetaWin: Statistical Software for Meta-Analysis. Version 2*. Sinauer Associates, Sunderland.

Rosenthal R. (2001) *Meta-Analytic Procedures for Social Research*. Sage Publications, Newbury Park.

Rosenthal R. & DiMatteo M. R. (2001) Meta-analysis: recent developments in quantitative methods for literature reviews. *Annu. Rev. Psychol.* **52,** 59–82.

Schechter E. (1997) *Handbook of Analysis and Its Foundations*. Academic Press, San Diego.

Semenov Y., Ramousse R., Le Berre M. & Tutukarov Y. (2001) Impact of the black-capped marmot (*Marmota camtschatica bungei*) on floristic diversity of Arctic tundra in Northern Siberia. *Arct. Antarct. Alp. Res.* **33,** 204–10.

Shea K., Roxburgh S. H. & Rauschert E. S. J. (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol. Lett.* **7,** 491–508.

Smith A. T. & Foggin J. M. (1999) The plateau pika (*Ochotona curzoniae*) is a keystone species for biodiversity on the Tibetan plateau. *Anim. Conserv.* **2,** 235–40.

Tews J., Brose U., Grimm V. *et al.* (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J. Biogeogr.* **31,** 79–92.

Waterman J. M. & Roth J. D. (2007) Interspecific associations of Cape ground squirrels with two mongoose species: benefit or cost? *Behav. Ecol. Sociobiol.* **61,** 1675–83.

Wesche K., Nadrowski K. & Retzer V. (2007) Habitat engineering under dry conditions: the impact of pika (*Ochotona pallasi*) on vegetation and site conditions in southern Mongolian steppes. *J. Veg. Sci.* **18,** 665–74.

Whitford W. G. & Kay F. R. (1999) Biopedturbation by mammals in deserts: a review. *J. Arid Environ.* **41,** 203–30.

Whittaker R. J., Willis K. J. & Field R. (2001) Scale and species richness: towards a general hierarchical theory of species diversity. *J. Biogeogr.* **28,** 453–70.

Wilby A., Shachak M. & Boeken B. (2001) Integration of ecosystem engineering and trophic effects of herbivores. *Oikos* **92,** 436–44.

Williams D. F. & Kilburn K. S. (1991) Dipodomys ingens. *Mamm. Species* **377,** 1–7.

Williams L. R. & Cameron G. N. (1991) Geomys attwateri. *Mamm. Species* **382,** 1–5.

Wright J. P. (2009) Linking populations to landscapes: richness scenarios resulting from changes in the dynamics of an ecosystem engineer. *Ecology* **90,** 3418–29.

Wright J. P. & Jones C. G. (2004) Predicting effects of ecosystem engineers on patch-sclae species richness from primary productivity. *Ecology* **85,** 2071–81.

Zenuto R. R. & Busch C. (1995) Influence of subterranean rodent *Ctenomys australis* (Tuco-tuco) in a sand-dune grassland. *J. Mammal. Biol.* **60,** 277–85.

Zhang Y., Zhang Z. & Liu J. (2003) Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. *Mamm. Rev.* **33,** 284–94.

SUPPORTING INFORMATION

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

Appendix S1. Richness, diversity and biomass entries.

doi:10.1111/j.1442-9993.2012.02403.x