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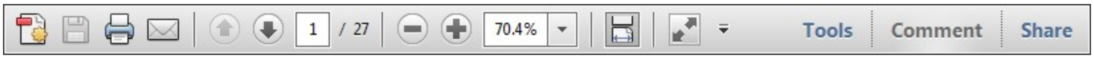

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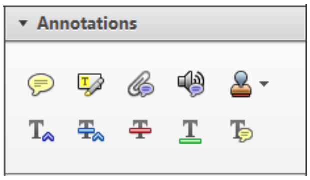

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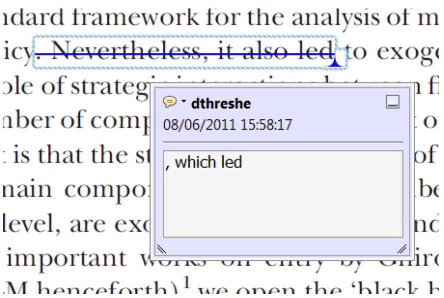

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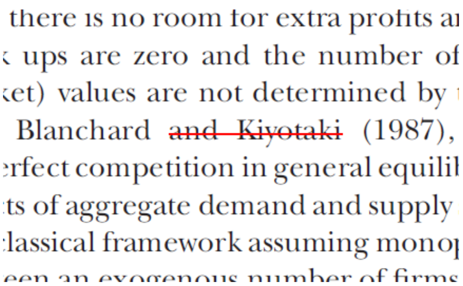

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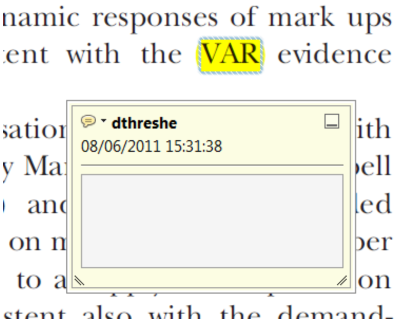

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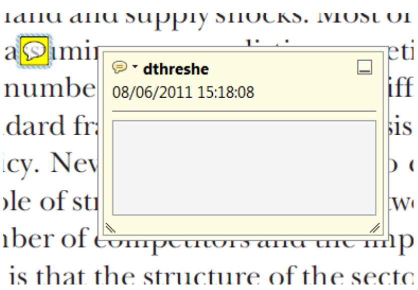

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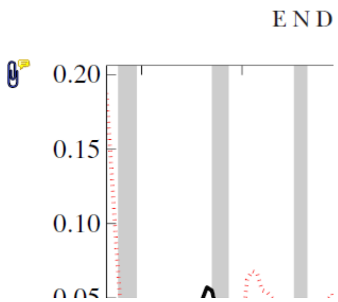

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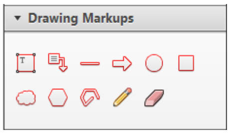

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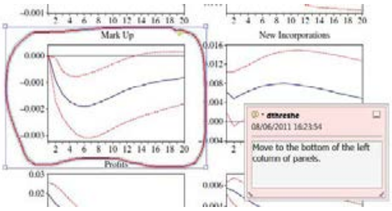

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The effects of ant nests on soil fertility and plant performance: a meta-analysis

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Summary

1. Ants are recognized as one of the major sources of soil disturbance world-wide. However, this view is largely based on isolated studies and qualitative reviews. Here, for the first time, we quantitatively determined whether ant nests affect soil fertility and plant performance, and identified the possible sources of variation of these effects.

2. Using Bayesian mixed-models meta-analysis, we tested the hypotheses that ant effects on soil fertility and plant performance depend on the substrate sampled, ant feeding type, latitude, habitat and the plant response variable measured.

3. Ant nests showed higher nutrient and cation content than adjacent non-nest soil samples, but similar pH. Nutrient content was higher in ant refuse materials than in nest soils. The fertilizer effect of ant nests was also higher in dry habitats than in grasslands or savannas. Cation content was higher in nests of plant-feeding ants than in nests of omnivorous species, and lower in nests from agro-ecosystems than in nests from any other habitat.

4. Plants showed higher green/root biomass and fitness on ant nests soils than in adjacent, non-nest sites; but plant density and diversity were unaffected by the presence of ant nests. Root growth was particularly higher in refuse materials than in ant nest soils, in leaf-cutting ant nests and in deserts habitats.

5. Our results confirm the major role of ant nests in influencing soil fertility and vegetation patterns and provide information about the factors that mediate these effects. First, ant nests improve soil fertility mainly through the accumulation of refuse materials. Thus, different refuse dump locations (external or in underground nest chambers) could benefit different vegetation life-forms. Second, ant nests could increase plant diversity at larger spatial scales only if the identity of favoured plants changes along environmental gradients (i.e. enhancing β-diversity). Third, ant species that feed on plants play a relevant role fertilizing soils, which may balance their known influence as primary consumers. Fourth, the effects of ant nests as fertility islands are larger in arid lands, possibly because fertility is intrinsically lower in these habitats. Overall, this study provide novel and quantitative evidence confirming that ant nests are key soil modifiers, emphasizing their role as ecological engineers.

Key-words: ants, ecological engineers, soil disturbance

Introduction

Small-scale disturbances are key factors influencing the structure and composition of communities. Disturbances often reduce the cover of dominant species and change resource availability, creating space and patchily distributed resources that can be used by subordinate and/or resource specialists' species (Pickett & White 1985). Specifically, soil disturbance by animals can directly impact vegetation, modifying the performance, abundance and richness of plants. Many animals create small-scale disturbances that have important ecological consequences through soil perturbations including agoutis, wild pigs, rabbits, armadillos, termites and ants, among others (Clark 1990; James, Eldridge & Hill 2009; Brody *et al.* 2010; Fox-Dobbs *et al.* 2010). Of these, ants are recognized as one of the major sources of soil disturbance world-wide because of their great diversity and abundance, wide geographical distribution and social

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4 behaviour (Folgaratit 1998; Frouz & Jilková 2008; Fig. 1). Ants are one of the most diverse group of social insects with an estimated of 25 000 species, is a dominant taxon of the terrestrial fauna accounting for large percentage of the total animal biomass, and occupy almost every continent (Hölldobler & Wilson 1990; Del Toro, Ribbons & Pelini 2012; Ward 2014). Ants often clear the soil surface of vegetation and mobilize large amount of underground soil to superficial layers to construct and maintain their nests. They also concentrate organic matter and produce large quantities of organic waste that are deposited inside the nest in specific chambers or on the soil surface. Because of these activities, ant nest soils show particular physical and chemical properties affecting the surrounding vegetation (Hölldobler & Wilson 1990; Folgaratit 1998; Fig. 1). Therefore, ant nests are considered one of the key small-scale disturbances (Lavelle *et al*. 1997; Leal, Wirth & Tabarelli 2014; Farji-Brener & Werenkraut 2015).

Although several works demonstrated the effects of ants on soil properties and vegetation patterns, there is conflicting evidence on whether these effects increase or decrease the nutrient content of soils, and if this, in turn, can influence plants growth. While most studies showed an increase in organic matter and soil nutrients in ant nest sites (Salem and Hole 1968; Czerwinsky *et al*. 1969; 5 6 Sorenson 1982; Frouz, Kalcik & Cudlin 2005; Farji- 7 Brener & Ghermandi 2008; Wagner & Nicklen 2010), some found the opposite trend (Dostal *et al*. 2005), or an increase in the level of some nutrients but a decrease in others (Beattie & Culver 1983; Wagner, Brown & Gordon 8 1997; Véle *et al*. 2010). Accordingly, there is contrasting evidence on whether plants growing around ant nests increase their performance and/or abundance (Horvitz & Schemske 1986; Whitford & Di Marco 1995; Wagner 1997; Frouz *et al*. 2008; Farji-Brener, Lescano & Gher- 9 mandi 2010; Saha *et al*. 2012), and the effects of ant nests on plant diversity (Beattie & Culver 1977, 1983; King 1977; Lewis, Franceschi & Stofella 1991; Farji-Brener & Ghermandi 2000). Unfortunately, the few studies that summarize these topics use a qualitative rather than a quantitative approach (De Bruyn & Conacher 1990; Folgaratit 1998; Del Toro, Ribbons & Pelini 2012) or focus

35 **Fig. 1.** Examples of ant nests as soil disturbances. Nests of (a) *Pogonomyrmex barbatus*, Arizona, USA; (b) *Myrmecocystus mexicanus* in Arizona, USA; (c) *Formica obscuripes*, California, USA; (d) *Dorymyrmex bureni*, Florida, USA; (e) *Camponotus termitarius*, Entre Ríos, Argentina; (f) *Atta wollenveideri*, Corrientes, Argentina; (g) *Acromyrmex lobicornis*, Patagonia, Argentina and (h) *Atta cephalotes*, Sarapiquí, Costa Rica. Photos credits: a–e ©Alex Wild, used by permission; f–h by AG Farji-Brener.

on a single ant group (leaf-cutting ants, Farji-Brener & Werenkraut 2015). Studying the effects of nests from a single ant group may underestimate their ecological relevance. For example, leaf-cutting ants are restricted to America, only feed on plant material and inhabit certain latitudinal ranges and habitats (Farji-Brener & Werenkraut 2015). To properly study the effects of ant nests on soil and plants, it is necessary to include all ant groups. Additionally, qualitative and anecdotic approaches are not enough to confirm the ecological effects of ant nests, estimate their strength and test hypotheses about their potential causes. Here, for the first time, we complemented these qualitative reviews with a meta-analysis of the literature analysing the effects of nests from all ant groups. Specifically, we quantitatively determined whether ant nests affect soil fertility and plant performance, and tested some hypotheses (see below) about the sources of variation of these effects.

The effect of ant nests on soil and plants could be affected by the substrate sampled, the ant feeding type, the geographical location of nests, the plant variable measured and the kind of data (e.g. field or greenhouse experiments). First, all ants generate organic waste. This refuse material is deposited in underground specific chambers or in external refuse piles depending on the species (Hölldobler & Wilson 1990). Given that there is some evidence that refuse material and nest soils may differ in their mineral content (Wagner 1997, Farji-Brener & Werenkraut 2015), the type of substrate sampled could partially explain the variation found in soil fertility around ant nests. Second, ants may feed on different items such as green plant material, seeds and dead or live arthropods (Hölldobler & Wilson 1990). Given that different food sources vary in their nutrient content (Lajtha & Michener 1994; Gannes, O'Brien & Martínez del Rio 1997), their accumulation inside the nest and the associated debris may influence the effect of ant nests on [10] soil chemistry (Shuklaa *et al.* 2013; Wu *et al.* 2013). Third, several abiotic and biotic characteristics change with latitude and among biomes affecting the ability of ants to improve soil fertility. For example, temperate regions and dry habitats often show extreme temperatures that may limit the ant foraging period (Whitford & Ettershank 1975; Lighton & Feener 1989), reducing their ability as soil modifiers. Furthermore, food items such as plants and arthropods vary in nutrient content, number and identity along geographical and environmental gradients (Oleksyn *et al.* 2003; Willig, Kaufman & Stevens 2003; Reich & Oleksyn 2004; Andrew & Hughes 2005; Lessard *et al.* 2011). As the effects of ants on soil fertility are strongly associated with the quality of stored food and produced debris (Tadey & Farji-Brener 2007), changes in food availability along latitudinal and environmental gradients may influence the extent of ant nests as soil disturbances. Finally, vegetation patterns may be affected by all the above discussed factors because plant performance and abundance are often influenced by soil fertility, but these effects may depend on the level of organization studied and the type of data. Enhanced nutrient patches could increase plant performance at individual and population levels, but may decrease plant diversity by favouring the dominance of few species at the community level (King 1977; Beattie & Culver 1983; Garretson *et al.* 1985). In addition, results from greenhouse [11] and field measurements may differ because plants in greenhouses are often under controlled conditions while field plants may suffer resource restrictions, environmental fluctuations and attacks by their natural enemies. In sum, all of these factors may influence the strength and sign of the impact of ant nests on soil fertility and plant performance, explaining the conflicting results obtained by different studies.

Here we quantitatively determine the effect of ant nests on soil fertility and plant performance using meta-analysis techniques. We also test the hypotheses that these effects depend on the substrate sampled (i.e. refuse material or ant nest soils), ant feeding type (leaf-cutting, granivore and omnivore), latitude (temperate, subtropical and tropical), habitat type (agro-ecosystems, humid forests, dry forests, desert shrublands or grasslands/savannas), the plant response variable measured (i.e. growth, reproduction, abundance and diversity) and the experimental design from which those data come from (i.e. greenhouse or the field).

Materials and methods

DATA COLLECTION

We identified relevant studies by examining the reference section of recent published papers on the topic and by conducting keyword searches in Biological Abstracts, Google Scholar and Current Contents databases using the words 'ant nests' and/or 'soil fertility' and/or 'soil nutrients' and/or 'ant nests effect on plants'. We also included our own unpublished records. We only included studies (i) that compared soil fertility and/or plant traits and/or plant richness between ant nest sites (treatment) and adjacent, non-nest sites (control); (ii) that reported means, sample sizes and standard errors (SE) or standard deviations (SD) for treatment and control to calculate effect sizes; and (iii) where ants identity was clearly established to be able to control for the species effect (see below). Our final database included 106 independent studies conducted between 1971 and 2015 (Appendix S1, Supporting Information). These 106 independent studies included 103 works from published literature and 3 from our own unpublished records; 49 of those studies reported ant effects on soil fertility, 29 on soil fertility and plant traits, and 28 only on plant traits. Therefore, the effect of ants on soil fertility was tested using 78 independent studies, and their effects on plant traits using 57 independent studies. This number of studies is among the range of replicates used in other meta-analyses (see Koricheva 2002; Morales & Traveset 2009; Winfree *et al.* 2009; Endara & Coley 2011, among others). Overall, our database included studies on 50 ant species from 18 genera distributed along a large latitudinal range and habitat types (see Appendix S1).

STATISTICAL ANALYSIS

We converted each pair of treatment and control observations from primary studies into a Hedges' *d* effect size, and its associated variance 'Var (*d*)' using metafor package (Viechtbauer 2010) in R software version 3.0.2 (R Development Core Team 2012). Hedges'*d* is an estimate of the standardized mean difference that is not biased by small sample sizes (Hedges & Olkin [12] 2014). An effect size of zero implies similar fertility/plant performance between nest and control sites, a positive *d* means higher soil fertility/plant performance in nest sites compared with non-nest sites, and negative values indicate the opposite trend.

Primary studies often contributed several effect sizes (e.g. measures of different soil nutrients from the same substrate sample) which may violate the assumption of independence. Additionally, another potential source of non-independence could arise from the use of multiple effect sizes from the same ant species (Borenstein *et al*. 2009; Mengersen, Schmidt & Jennions 2013). We thus applied hierarchical meta-analysis, using study and species as random factors, to effectively partition correlation structures within these levels (Nakagawa & Santos 2012). Incorporating this variance structure allowed our 106-study dataset to provide 361 and 121 effect sizes for soil fertility and plant performance analyses respectively, without violating independence assumptions. For each effect size, we recorded additional information on other variables that were treated as moderators. These included: (i) substrate: whether soil fertility or plant traits were measured on nest soils or on refuse dumps; (ii) latitude: whether ant nests were in tropical, subtropical or temperate regions; (iii) ant feeding type: whether ants were leaf-cutters, omnivores or granivores; (iv) habitat type: whether ant nests were located in agro-ecosystems, humid forests, dry forests, desert shrublands or grasslands/savannas; and (v) experimental design: whether plant traits were measured in a greenhouse or in the field.

We evaluated how ant nests affect different characteristics of soil fertility and plant performance. We performed separated meta-analyses to evaluate the effect of ant nests on: (a) soil nutrient content (C, N, P and K), (b) soil cation content (Al, Ca, Mg and Na), (c) soil pH, (d) plant green growth (e.g. steam diameter, leaf biomass and/or plant height), (e) plant root growth (e.g. root biomass and root dry weight), (f) plant reproduction (e.g. number of seeds per plant and fruit density), (g) plant density (e.g. plant cover and/or individuals/area) and (h) plant species richness (plant species/area). Thus, we evaluated the effect of ant nests on plants at individual (d–f), population (g) and community levels (h). We estimated the overall effect size for each focal trait running mixed-effects models without predictors using *species* and *paper* as random effects.

For each soil fertility and plant performance trait, we used a meta-regression approach to account for variations in different levels of the moderator variables listed above (i.e. substrate, latitude, etc.). It would be ideal to evaluate how multiple potential predictors may influence ant nest effect on soil fertility and plant performance. Unfortunately, for our focal soil and plant traits, several of our predictors were partially collinear. For instance, all studies that tested pH differences between ant nests and control soils in seed-harvester ants were made on temperate latitudes, and most of the studies that evaluated differences in soil nutrient content induced by seed-harvester ants were tested on refuse dumps (59 of 61 observations). Due to this limitation, and in order to avoid model over-parameterization, for each focal trait, we decided to test each moderator variable using *univariate* models in which the focal predictor was included as a fixed effect, along with *species* and *study* (i.e. paper) as random effects. We were unable to test some combinations of focal traits and moderator variables due to insufficient data points in each category (e.g. only one study measured cation content on dry forests, see Results). Therefore, a potential bias of our results is that the effects of these partially collinear predictors cannot be fully distinguished. Nonetheless, we can describe which factors were associated with variation in effect sizes, and based on our results, we discuss future experiments that can better disentangle these patterns (see Discussion).

We performed all the analysis running Bayesian mixed-models with a normal error distribution, using Markov Chain Monte Carlo (MCMC) techniques from MCMCglmm package (Hadfield 2010) in R software version 3.0.2 (R Development Core Team 2012). These models allowed us to statistically control for correlated variation arising from species and study identity by stating them as random effects, and modelled residual variance (within-study variance) in addition to sampling error variance (measurement variance). For all models, we ran 5 000 000 MCMC iterations, with a burn-in period of 4 000 000, and a thinning interval of 1000. We used uninformative inverse gamma priors for the random effects ($V = 1$, $nu = 0{\cdot}002$). For each model, we ran three independent MCMC chains using different starting values. We checked the convergence of each analysis by visual inspection of the posterior distribution, by exploring the autocorrelation among subsequent lags within chains, and using Gelman–Rubin diagnostic test (potential scale reduction factor [PSR]; Gelman & Rubin 1992) among the three chains in the R package 'coda' (Plummer *et al*. 2006). All models converged, presenting MCMC chains with an autocorrelation of less than 0·1, and producing a PSRs lower than 1·1. Bayesian statistics uses Bayes' rule to update beliefs about parameters (prior distributions) in the light of data and a probability model (likelihood function). Updated knowledge about parameters is represented in the posterior distribution (Gelman *et al*. 2014). From the posterior distribution, it is possible to quantify the uncertainty around parameter estimates via credible intervals (CRI). Contrary to a frequentist confidence interval, a CRI is a direct probability statement about an unknown parameter. There are different methods to define a CRI on a posterior distribution (Link & Barker 2010). One particular case is the highest posterior density interval (HPD), which is the interval delimited so that it includes the highest possible posterior density. Here we report posterior estimates means and 95% HPD interval for meta-analytic model's intercepts and slopes. We consider that there is strong evidence about an effect size being different from zero, when its 95% HPD does not span zero. To test differences between two levels of a moderator variable, we compute the extent of overlap between their posterior distributions (OBP). We inferred differences between the two levels when the OBP was less than 5%. To quantify heterogeneity, we used a modified version of I^2 (Higgins & Thompson 2002) following Nakagawa & Santos (2012), which is suitable for multilevel meta-analytic models. [13] Heterogeneity was partitioned between each random factor and residuals, and total heterogeneity was the percentage of total variance explained by all random factors and residuals. I^2 values of around 25%, 50% and 75% are considered as low, moderate and high levels of heterogeneity, respectively (Higgins *et al*. 2003).

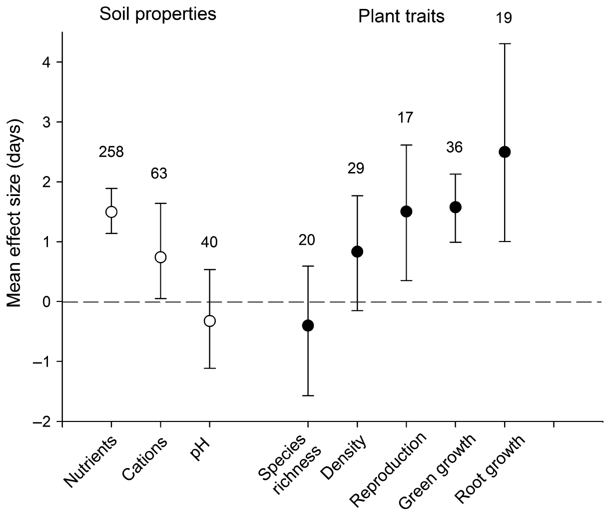

Fig. 2. Mean effect size (Hedge's *d*) and 95% highest posterior density intervals of the effect of ant nests on soil properties and plant traits. Numbers indicate sample sizes.

PUBLICATION BIAS

We tested for publication bias (i.e. the tendency of journals to favour publication of statistically significant results) through visual inspection of funnel plots, by conducting trim and fill assessments and Egger's regression analysis (Egger *et al.* 1997). Owing that our data were heterogeneous and non-independent, to produce funnel plots, we plotted meta-analytic models residuals vs. precision, and we used a modified version of Egger's regression following Nakagawa & Santos (2012). Trim and fill tests were conducted on the models' residuals using the trimfill function from METAFOR package (Viechtbauer 2010) in R software version 3.0.2 (R Development Core Team 2012). When trim and fill analyses suggested evidence of publication bias, we performed a sensitivity analyses adjusting the original meta-analytic mean and CI by subtracting the trim and fill estimate to evaluate the robustness of our result (Sutton *et al.* 2011; Nakagawa & Santos 2012).

Results

GENERAL EFFECTS

Overall, the presence of ant nests increased soil nutrient and cation contents, and had no effects on soil pH (Fig. 1, Appendix S2: Table S1a). On the other hand, nest areas showed higher plant growth and plant reproduction, but similar plant density and plant richness than adjacent non-nest soils (Fig. 2, Appendix S2: Table S1b).

EFFECTS OF MODERATOR VARIABLES

We explored the effect of moderators on soil properties and plant performance traits that showed an effect (i.e. its 95% HPD does not overlap zero). We were unable to test the effect of moderators on plant reproduction due to the low number of effect sizes recorded.

Nutrients

Nutrient content was higher on ant nests than in control sites for both substrate types (i.e. refuse material and nest soil), in all latitudes, for all feeding types, and in humid forests, desert shrublands and grasslands/savannas (Fig. 3, Appendix S2: Table S3). Refuse material had higher nutrient content than nest soils; and desert shrublands had higher nutrient content than grasslands/savannas (Fig. 3). Nutrient content was unaffected by latitude (Appendix S2: Table S4), or ant feeding type (Appendix S2: Table S4).

Cations

Cation content was higher on ant nests than in control sites when it was measured on refuse material, from leaf cutter ant nests, and marginally in soils from humid forests; but showed the opposite trend in agro-ecosystems (Fig. 4, Appendix S2: Table S3). Refuse material had similar cation content than nest soils. Subtropical, temperate and tropical nest sites did not differ in cation content (Appendix S2: Table S4). Leaf cutter ant nests had higher cation content than omnivorous ant nests, but similar cation content than granivorours ant nests. Agro-ecosystems had less cation content than any other habitat (Appendix S2: Table S4).

Plant performance

Green growth was higher in plants growing on ant nests than in control sites for both substrate types (Fig. 5), in temperate latitudes, for all feeding types, in desert shrublands, and for both types of data (i.e. from greenhouse and the field) (Fig. 5a, Appendix S2: Table S3). Root growth was higher on ant nests than in control sites in plants growing on refuse material, in temperate and tropical latitudes (not enough data were available to test the effect on subtropical latitudes), on leaf cutter ant nests and in desert shrublands habitats (Fig. 5b, Appendix S2: Table S3). Plant growth was unaffected by substrate type, latitude, ant feeding type, habitat and rearing conditions (Fig. 5, Appendix S2: Table S4).

HETEROGENEITY AND PUBLICATION BIAS

When we evaluated the overall effect of ant nests on soil properties and plant performance, we observed high heterogeneity among effect sizes despite many studies showed a clear effect of ant nests ($I^2_{[\text{total}]}$ from 71% to 97%; Appendix S2: Tables S2). The random terms considered, explained a small part of the variation (between-study variation, $I^2_{[\text{study}]}$ from 11% to 35%; between-species variation, $I^2_{[\text{species}]} = 5$–19%). Most of the variance was accounted for by within-study variation ($I^2_{[\text{residual}]}$ from 41% to 79%; Appendix S2: Table S2).

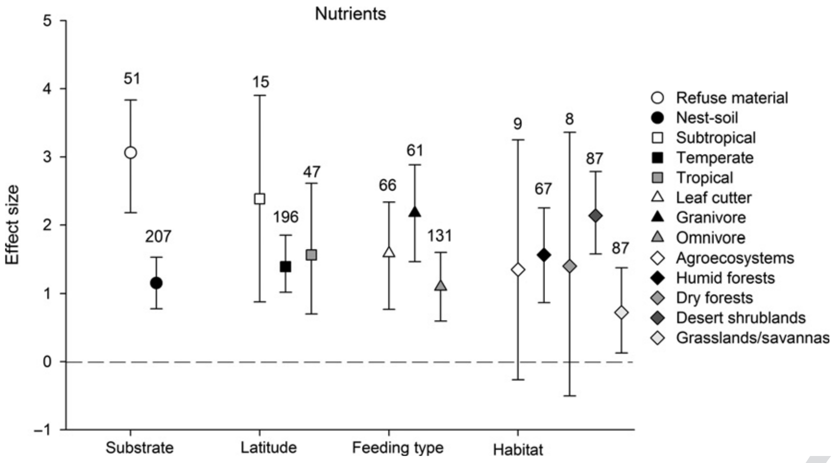

Fig. 3. Mean effect size (Hedge's *d*) and 95% highest posterior density intervals of the effect of ant nests on nutrients depending on type of substrate, latitude, ant feeding type and habitat. Numbers indicate sample sizes for each category.

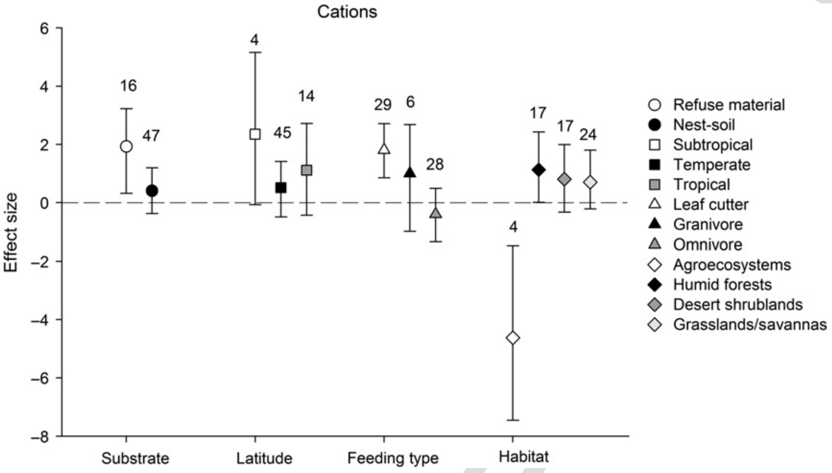

Fig. 4. Mean effect size (Hedge's *d*) and 95% highest posterior density intervals of the effect of ant nests on cations depending on type of substrate, latitude, ant feeding type and habitat. Numbers indicate sample sizes for each category.

We found some evidence of publication bias. Visual inspection of funnel plots revealed some degree of asymmetry for all traits except for plant density and plant green growth (Appendix S3: Fig. S1). Trim and fill method added 7, 3, 1, 2 and 5 points to the original number of effect sizes for nutrient content, pH, plant species richness, plant reproduction and plant root growth respectively (Appendix S3: Fig. S2, Table S1). Adjusting our meta-analytic means by trim and fill estimates did not quantitatively alter our original estimates (Appendix S3: Table S1). Publication bias found via Egger's regression slightly differed from the one found using trim and fill analysis (Appendix S3: Table S1).

Discussion

Ant nests have been considered one of the most important small-scale disturbances affecting both soil conditions and vegetation patterns, but these assertions were based on studies on a single ant group (leaf-cutting ants, Farji-Brener & Werenkraut 2015) and qualitative reviews (De Bruyn & Conacher 1990; Folgaratit 1998; Del Toro, Ribbons & Pelini 2012). Here, for the first time, we quantitatively analysed the effects of nests of all ant groups on soil and plants and determined some of their source of variation. Several patterns and trends emerge from our study. First, ant nests improve soil fertility through an increment in the levels of nutrients and cations without affecting soil pH. The sampled substrate, habitat and ant feeding type influence the magnitude of these effects. Second, the presence of these nutrient-rich spots increases plant performance and fitness but not plant abundance or diversity. The strength of these effects (mainly on root growth) depends on the sampled substrate, ant feeding type and habitat. Taken together, this quantitative evidence confirms the major role of ant nests influencing soil fertility and vegetation patterns.

The first finding of this work is the confirmation that ant nests are hot-spots of soil fertility, and the key role of refuse material on this effect. We found that the ant-generated refuse material is several times richer in nutrients and cations than the nest soil itself, expanding the pattern already found in leaf-cutting ants to other ant feeding types (Farji-Brener & Werenkraut 2015). Two reasons may explain why nest soils could be less fertile than ant refuse materials. First, during nest construction and growth ants can transport mineral soil with low nutrient concentration to the nest surface (Alvarado, Berish &

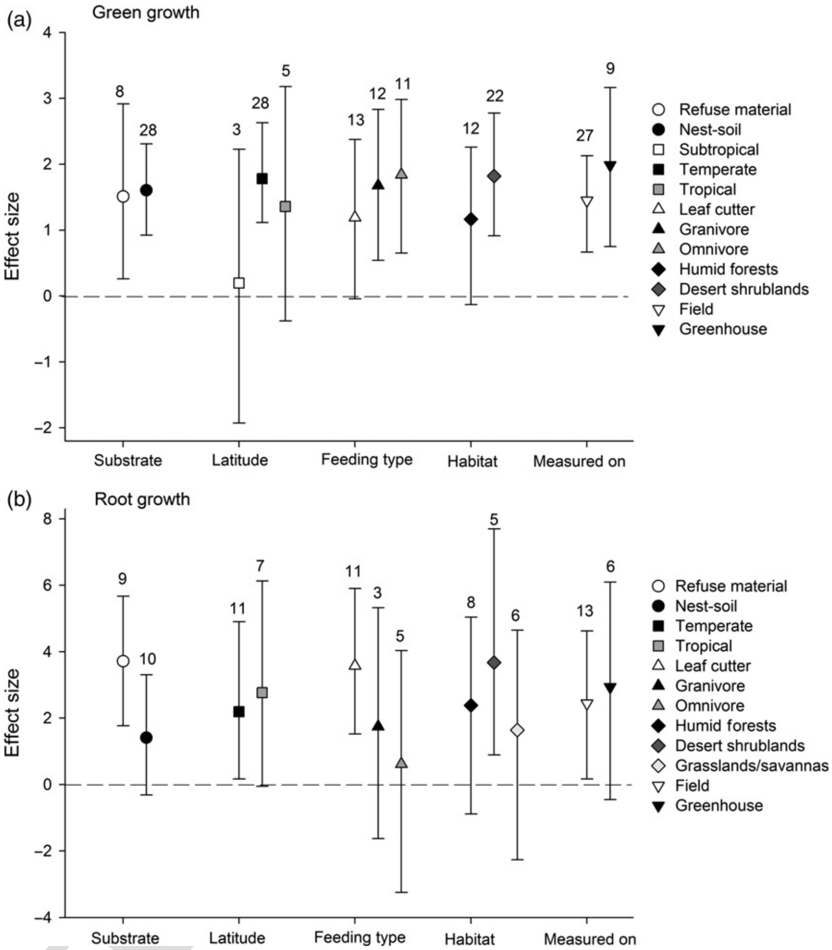

Fig. 5. Mean effect size (Hedge's *d*) and 95% highest posterior density intervals of the effect of ant nests on plant (a) green growth and (b) root growth depending on type of substrate, latitude, ant feeding type, habitat and the where the data come from (greenhouse or field measurements). Numbers indicate sample sizes for each category.

Peralta 1981). Second, ants heavily harvest almost all plants around the nest area, reducing the amount of leaf litter falling on nest top soils (Farji-Brener & Illes 2000; Hull-Sanders & Howard 2003). On the other hand, as explained earlier, refuse materials are mainly composed by organic matter that house high abundance and diversity of soil biota which is responsible for nutrient mineralization (Farji-Brener 2010; Sousa-Souto *et al.* 2012; Fernández, Farji-Brener & Satti 2014). Refuse materials also show higher levels of nutrient content than cations. This may arise from the fact that nutrients such as N, P and K come from organic sources, while cations mainly from minerals. Thus, the amount, quality and location of the refuse should be of special interest for a better understanding of the ant nest fertility effects (Leal, Wirth & Tabarelli 2014).

The feeding type of ants and habitat also influence the strength of ant nests as 'fertility islands'. Leaf-cutting and granivorous ants contribute more to soil fertility than omnivorous species, suggesting that the accumulation of food and waste generated from plant sources improves soil fertility more than that coming from animal sources. This pattern can be attributed to the considerably larger quantities of plant vs. animal biomass in most terrestrial ecosystems, and to the known differences between plants and animals in tissue characteristics, nutritional composition and decomposition rate (Parmenter & MacMahon 2009). The considerable size of leaf-cutting and granivorous ant colonies may also contribute to their key role enhancing soil fertility (Hölldobler & Wilson 1990). Habitat type also influences the contribution of ant nests on soil properties. Ant nests in dry environments enhance soil nutrients more than ant nests on grasslands or savannas, and ant nests in agro-ecosystems show less cation content than adjacent, non-nest soils. The higher contribution of ant nests in dry habitats may be consequence of two associated factors. On the one hand, soil nutrients are key limiting factors in dry habitats, highlighting the effect of ant nests as soil nutrient sources (Satti *et al.* 2003; Tadey & Farji-Brener 2007). Second, plant species from drier sites often show higher N and P content than those from humid sites (Wright, Reich & Westoby 2001; Oleksyn *et al.* 2003; Reich & Oleksyn 2004; Lovelock *et al.* 2007). As plant material and plant-feeders are the key food sources for ants, the nutrient quality of the accumulated food and produced refuse may be relatively higher in arid than in humid environments. We also found that cation content in agro-ecosystems nests is lower than in adjacent non-nest sites. One possible cause is that the fertilizer addition typical of agro-ecosystems hides the fertilizer effect of ant nests. However, given the low number of works studying ant nest effects in this habitat (n = 4), this interpretation should be treated with caution. Overall, ant nests can be considered as 'islands of soil fertility' mainly via the generation of refuse materials, and particularly relevant in ant species that feed on plant sources (leaf-cutting and granivorous ants) and in dry habitats.

The second finding of this work is that ant nests enhance plant performance, but their presence does not affect plant density or diversity. By tracing radioactive or stable isotope-labelled substances, numerous studies have found evidence of nutrient absorption from ant nests to plant tissues (Rico-Gray *et al*. 1989; Treseder, Davidson & Ehleringer 1995; Sagers, Ginger & Evans 2000; Sternberg *et al*. 2007; Farji-Brener & Ghermandi 2008; Wagner & Nicklen 2010; Lescano *et al*. 2012). This nutrient input often increases the growth rate and the fitness of plants (Rissing 1986; Wagner & Nicklen 2010; Farji-Brener & Werenkraut 2015). As we showed that ant nest sites are 'fertility islands', it is logical that plants established on ant nests grow better and showed more fitness than those growing on non-nest soils. This positive effect of ant nests on individual plants apparently does not extend to population and community levels. It is known that not all plant species respond equally to the excess of soil resources (Farji-Brener, Lescano & Ghermandi 2010). Moreover, the physical characteristics of ant nests and the changes in microclimatic conditions generated by ant activities may act as ecological filters for plant recruitment disfavouring or favouring particular species (Garrettson *et al*. 1998; Farji-Brener 2005; Silva *et al*. 2012; Leal, Wirth & Tabarelli 2014). We also found that the strength of these effects depends on the substrate sampled, ant feeding type and habitat. Specifically, root growth is particularly enhanced in plants growing on refuse materials, leaf-cutting ant nests and dry habitats. As we showed that refuse materials have higher nutrient content than nest soils, it is reasonable that the roots that access this substrate show greater growth (Farji-Brener & Ghermandi 2008; Farji-Brener, Lescano & Ghermandi 2010). The huge production of refuse material, high ant density and colossal dimensions of leaf-cutting ant nests may enhance this process (Farji-Brener & Werenkraut 2015). Finally, as soils of dry habitats are markedly nutrient-limited (Havstad, Herrick & Schlesinger 2000; Satti *et al*. 2003; Woker 14 *et al*. 2005), the fertility effect of ant nest in this habitat is probably highlighted.

Overall, the results of our meta-analysis confirm certain patterns obtained for anecdotal and/or isolated studies and reveal some of their sources of variation, helping to better understand the key role of ant nests on ecosystems. We summarize them as follows. First, as ant nests improve soil fertility mainly through the accumulation of refuse material, the vegetation life-form affected and the ecological impact of these effects will finally depend on the location of this key nutrient source. External refuse piles are temporarily unstable because of wind and rain, but are easily available by seedlings and small plants. Conversely, refuse material in underground nest chambers are more long-lasting but only large tree roots can access them (Moutinho, Nepstad & Davidson 2003; Saha *et al*. 2012). This pattern is well known for leaf-cutting ants, where nests with inner refuse chambers are often colonized by trees, promoting the formation of woody 'islands' in grass-dominated savannas and pastures (Jonkman 1978; Farji Brener & Silva 1995; Sosa & Brazeiro 2012). Meanwhile, ant nests with external refuse dumps are often colonized by short-living plants (Farji-Brener & Ghermandi 2004, 2008). Thus, the location of refuse material might determine the role of ant nests on plants. Second, ant nests may improve plant diversity at larger spatial scales. Despite nest sites do not necessarily harbour more floral diversity than adjacent non-nest sites, the vegetation that mainly grows on nest sites can differ along geographical gradients. Therefore, ant nests may increase beta diversity and enhance plant richness at a landscape level. Third, ant species that feed on plants play a relevant role in fertilizing soils, which may balance their known influence as herbivores. The role of leaf-cutting and granivorous ants as top-down forces regulating primary production is widely known (MacMahon, Mull & 15 Crist 2000; Wirth *et al*. 2003; Costa *et al*. 2008). Here we also confirm the key role of these ant groups as bottom-up forces through soil nutrient improvement. Fourth, our results reinforce the relevance of ants in desert ecosystems. Several works highlight the negative impacts of ants on plants in desert areas (Brown, Reichman & Davidson 1979; Costa *et al*. 2008; Pirk & Lopez De Casenave 2014). We complement these findings highlighting the positive influence of ants that inhabit desert lands on soil fertility and vegetation performance.

Experimental evidence of the key role of ants in ecosystems is often scarce but consistent. All field exclusion of ants demonstrated that they are crucial in ecosystem functions such as nutrient cycling, soil respiration, seed removal and invertebrate predation (Del Toro *et al*. 2015, 16 Ewers *et al*. 2015). For example, the presence of ants reduced the decline of total nitrogen by ~9 mg kg^{-1}, which corresponds to around 8 kg nitrogen per ha (Evans *et al*. 2011). Here we provide novel, quantitative evidence suggesting that these effects are quite general across several ant groups and habitats. To complement our findings, additional data on nest size, nest density and the rate of refuse production are needed from a wide range of ant species and habitats. Despite this need of more information, our meta-analysis confirmed that ants are one outstanding example of world-wide ecosystem engineers (*sensu* Jones *et al*. 1997) because their nests physically 17 modify their surroundings creating habitat for other organisms.

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Data accessibility

The database is at the Appendixes.

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Supporting Information

Details of electronic Supporting Information are provided below.

Appendix S1. Studies included in the meta-analysis.

Appendix S2. Supplementary results.

Appendix S3. Publication bias. 34

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