Pervasive and strong effects of plants on soil chemistry: a meta-analysis of individual plant 'Zinke' effects

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Abstract

Plant species leave a chemical signature in the soils below them, generating fine-scale spatial variation that drives ecological processes. Since the publication of a seminal paper on plant-mediated soil heterogeneity by Paul Zinke in 1962, a robust literature has developed examining effects of individual plants on their local environments (individual plant effects). Here, we synthesize this work using meta-analysis to show that plant effects are strong and pervasive across ecosystems on six continents. Overall, soil properties beneath individual plants differ from those of neighbours by an average of 41%. Although the magnitudes of individual plant effects exhibit weak relationships with climate and latitude, they are significantly stronger in deserts and tundra than forests, and weaker in intensively managed ecosystems. The ubiquitous effects of plant individuals and species on local soil properties imply that individual plant effects have a role in plant–soil feedbacks, linking individual plants with biogeochemical processes at the ecosystem scale.

1. Introduction

Plant effects on soil properties generate heterogeneity in biogeochemical patterns and processes at multiple spatial scales, from the individual tree canopy to the landscape. The mechanisms that underlie plant effects on

soil chemistry are well known: plants take up water and mineral nutrients through their roots, and deliver organic matter back to the soil via litterfall, roots and root exudates [1,2]. When plants strongly affect nutrient cycling beneath their canopies, ecosystem-scale nutrient budgets are strongly influenced by the relative abundance and size of plant species [3,4]. Additionally, in spatially heterogeneous soils, source–sink dynamics between resource-rich and resource-poor patches can increase landscape-scale productivity [5]. Therefore, plant-generated spatial heterogeneity in soil processes is an important component of ecosystem-level estimates of biogeochemical processes [6].

In 1962, Zinke published a now classic paper [7] that remains one of the most elegant demonstrations of the effects of an individual plant on soil properties. Zinke found consistent patterns in soil properties moving from the bole to beyond the crown edge of a *Pinus contorta* tree. There are several important features of Zinke's 1962 paper: (i) it centres on individual organisms; (ii) it presents a mechanism that accounts for spatial patterns of soil chemical variables; and (iii) it implies that plant-generated soil heterogeneity at the scale of individuals affects ecological phenomena at the population, community and ecosystem levels. Here, we use the term 'individual plant effects' (which we refer to as IPEs for brevity) to refer to distinct signatures in soil chemistry beneath individual plants (e.g. trees, shrubs or perennial grasses), which result from variation in plant resource uptake, unique microbial communities, litter quantity, tissue quality of leaf and root litter, or some combination of these or other attributes. Our definition of individual plant effects is distinct from plant–soil feedbacks (PSFs), which are defined as plant-induced changes in soil properties that in turn affect plant growth or fitness [8]. By contrast, IPEs, as we define them, are spatially explicit and concern only the effects of plants on the soils beneath them, rather than the two-way relationship between soil properties and plant growth. In the decades following publication of Zinke's original paper, a robust literature on individual plant-induced soil heterogeneity has developed [1,2]. However, although the effects of individual plants on soil properties have been demonstrated conclusively in many ecosystems, few if any studies have examined their generality, the factors that regulate IPEs, or how they vary along abiotic and biotic gradients.

Abiotic factors and plant community composition have interactive effects on soil properties. For example, many studies of plant-induced soil heterogeneity are conducted under harsh abiotic conditions, where plants represent 'islands of fertility' in arid environments [9]. Temperature, precipitation and wind may directly affect plant–soil interactions by influencing the movement of plant litter and soil nutrients across the landscape [5]. Abiotic conditions also influence plant–soil interactions indirectly by shaping the morphology, physiology, functional attributes and species composition of plant communities. Plant effects on soil may be larger when plants exhibit strongly divergent root and foliar chemistry [3,10] or growth form [11]. By contrast, IPEs may be weaker in ecosystems where single-tree effects are diluted by closed canopies, diverse understoreys and an abundance of vines, such as many tropical forests [12].

Stand age can also modify the magnitude of plant-induced heterogeneity. Intuitively, IPEs should strengthen over the lifespan of an individual shrub or tree as plant litter accumulates and decomposes. This process would yield a positive relationship between stand age and the magnitude of IPEs, as has been observed in some studies [13]. Land use may also affect the strength of IPEs; for example, the influence of legume trees on soil properties was more pronounced in plantations than in nearby unmanaged forests, where understorey communities attenuated effects of legume-derived N inputs [14].

The magnitude of plant effects on soil properties may also vary depending upon the edaphic variable under study. Elements that are crucial for plant growth, such as potassium and phosphorus, are generally concentrated in shallower soil horizons [15]. Additionally, because foliar nutrient concentrations and nutrient resorption are dependent upon the relative availability of essential elements [16], IPEs may be stronger for the most limiting nutrients. Thus, plant-induced soil heterogeneity should be more pronounced in organic versus mineral soil horizons, and essential plant nutrients are more likely to be affected by vegetation than non-essential nutrients.

However, because some species can accumulate and exude heavy metals as a form of 'elemental allelopathy' [17], toxic or non-essential elements may actually show stronger spatial signatures than N, P and K in some environments. The relative mobility of different elements might also determine the extent to which plants control specific soil properties. For example, ions such as NO_3^-, which diffuse rapidly, should be more sensitive to plant presence than less mobile ions such as PO_4^{3-}, which may become strongly adsorbed to soil minerals.

In this study, we quantified the magnitude of individual plant-induced changes in soil chemistry (IPEs) along gradients of environmental conditions and plant community structure. We collated studies from the literature that have investigated plant-generated soil heterogeneity to address four specific hypotheses. Our first hypothesis was that plant effects on soil chemistry would be more pronounced in ecosystems where plant canopies are clearly delineated and do not overlap. Therefore, IPEs should be regulated directly by environmental conditions, with stronger plant–soil interactions under harsh abiotic conditions—that is, low mean annual temperature (MAT) and/or precipitation (figure 1), or in metal-enriched or acidic soils. Second, we hypothesized that IPEs would be sensitive to indirect effects of climate via plant community structure (i.e. the relative abundances of plants with different growth forms such as trees, shrubs, grasses versus bare soil). Additionally, plant influence on soil chemistry should be greater in patchy landscapes with plant canopies surrounded by a matrix of mineral soil versus ecosystems with continuous plant cover such as forests (figure 1). Third, we hypothesized that IPEs would increase with stand age, reflecting changes in the strength of plant–soil interactions over time. Finally, we hypothesized that IPEs would be stronger for nutrient elements (N, P, K, Ca and Mg) and weaker for non-essential elements or micronutrients (Al, Na, Zn) owing to tighter plant control over the cycling of essential resources.
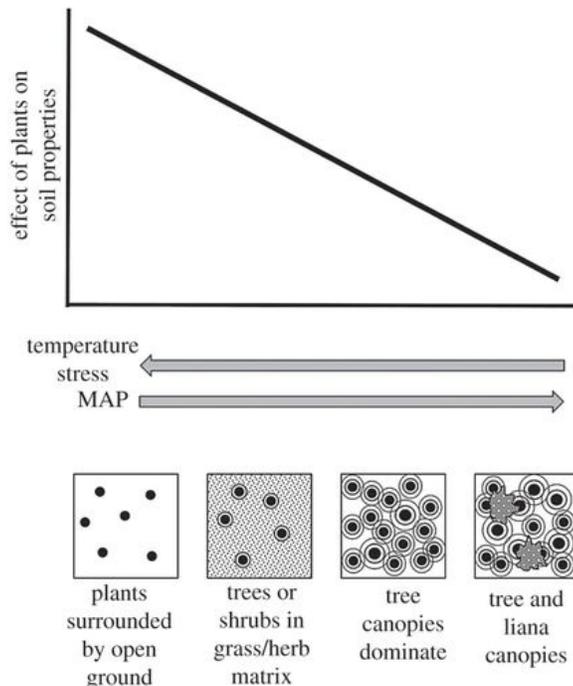

Figure 1. We hypothesized that the effects of plants on the soils beneath them should increase as a function of temperature and moisture stress, generating a relationship between individual plant effects and canopy cover.

2. Methods

(a) Data mining, extraction and coding
We assembled a comprehensive database on the effects of individual plants on soil properties searching the ISI Web of Science using the terms 'islands of fertility AND soil' or 'soil AND plant AND individual heterogeneity'

from 1962 until January 2011. We also examined all of the papers that cited the original Zinke paper [**7**] that appeared in Google Scholar through January 2011. Our initial search yielded approximately 300 papers. We restricted our database to studies that quantified soil properties in the field, and excluded experimental manipulations or laboratory studies. As the focus of our analysis is plant individual-generated soil heterogeneity, we also omitted studies where measurements were not taken at the scale of an individual plant canopy. Following our initial reading of these papers, we identified a second set of relevant papers from the cited references. This search resulted in 108 papers that matched our criteria (electronic supplementary material) and included studies that quantified soil properties beneath canopies of different plant species, at varying distances from an individual plant, or both.

For each publication, we recorded the latitude and longitude of study site(s), MAT and precipitation (MAP), the depth of the soil horizon(s) sampled, the plant species under study and any information about land-use history. Although most publications reported data collected at a single site, some compared plant–soil interactions at locations spanning broad environmental or biogeographic gradients. Therefore, for the purposes of this analysis, we defined a 'site' as a sampling area with a common soil type, climate and plant community.

Because organic and mineral soils vary greatly in element concentrations and microbial activity, we treated samples from organic versus mineral soil horizons separately. However, if data for multiple depth increments were reported within an organic or mineral horizon, we took the average treatment value across all depths. Additionally, if the same site was sampled at multiple times over the year, data were averaged across all sampling time points before effect size calculations. We classified each unique study site into an ecosystem category using MAP, MAT and latitude/elevation according to the Holdridge life zone scheme [**18**]. We then collapsed the resulting life zone categories into five unique biome types: desert, grassland, dry forest, wet/moist forest (temperate and tropical) and paramo/tundra (electronic supplementary material, table S1). Where information was available, we also assigned sites to one of three land-use categories to reflect degree of disturbance and anthropogenic influence: primary/undisturbed, secondary/regenerating or plantation/agroecosystem. Finally, we recorded focal plant growth form (tree, shrub, grass) and the surrounding matrix type: shrubs, grass or exposed mineral soil (in systems with patchy plant distributions and discontinuous O horizons). In closed-canopy forest ecosystems, matrix type was classified as 'none'.

(b) Soil variables

There are many different methods for measuring individual soil chemical variables. We distinguished between methods that involved soil digestion and presumably aimed at quantifying 'total' elements from methods that involved soil extractions, the latter presumably aimed at quantifying 'labile', 'extractable' or 'plant-available' nutrients. We grouped data measured according to the following methods: pH (measured in salt solutions or water), labile phosphorus (including P extracted with sodium bicarbonate, water, Olson's solution, Bray solution, bicarbonate-extractable organic P or resin P) and inorganic nitrogen (ammonium, nitrate or their sum, as well as net mineralization rates). Because there were no more than 10 observations for total Al, Ca, K, Mg and S, we did not distinguish between total and extractable pools of these elements in our analysis. The final list of soil variables appears in **table 1**.

Table 1. Mean effect sizes (IPEs) for each soil variable included in the dataset averaged over mineral and organic horizons. Upper and lower limits represent the bounds of the 95% CI.

variable	mean IPE (effect size)	lower limit	upper limit	sample size (no of studies)
Al	0.363	0.034	0.691	5
base saturation	0.594	0.356	0.832	9
bulk density	0.203	−0.019	0.425	9
C	0.354	0.260	0.448	59

Ca	0.500	0.410	0.591	53
CEC (cation exchange)	0.163	0.002	0.324	17
C : N	0.265	0.088	0.443	12
EC (electrical conductivity)	0.824	0.555	1.092	9
K	0.417	0.320	0.515	52
Mg	0.379	0.285	0.473	46
Na	0.274	0.125	0.423	23
N (inorganic)	0.495	0.394	0.596	37
N (total)	0.394	0.301	0.488	69
organic matter	0.366	0.252	0.480	35
P (extractable)	0.453	0.354	0.551	59
P (total)	0.263	0.122	0.403	16
pH	0.186	0.114	0.259	73
S	0.344	−0.054	0.742	4
soil moisture	0.114	−0.003	0.232	20
Zn	0.504	0.264	0.744	5

Some of the soil variables we examined are inherently more variable than others; for example, soil pH is restricted to a fairly narrow range as it is on a log scale, whereas inorganic N or labile P content can vary by orders of magnitude. Therefore, for each soil variable, we centred and scaled the data, so that the standard deviation of the response variable was equal to 1. (Results were qualitatively identical when unscaled variables were analysed, but these data are not reported here.)

(c) Quantification of effect sizes

We calculated an IPE size for every reported soil variable at each unique site within a study. For each site/soil variable combination, we recorded the mean values and sample size (n) for every plant treatment (species or distance from focal plant). Next, we generated a matrix of all possible pairwise comparisons among plant treatments. For each individual pairwise comparison, we calculated the IPE as

$$\ln \frac{Trt_A}{Trt_B}$$

$$\ln \frac{Trt_A}{Trt_B}$$

2.3

where Trt_i represents soil properties beneath an individual plant i. Because we were interested in the magnitude of the difference in soil properties beneath two plant types (i.e. comparisons between two species A and B) or the presence of a plant (comparisons between underneath focal plant A to non-plant area B), we calculated the IPEs such that the value of Trt A > Trt B. Therefore, all IPE estimates had a lower bound of 0 (i.e. identical soil properties between plant treatments). Finally, we averaged the IPEs generated from each matrix to determine the mean log response ratio and its standard deviation. Therefore, our final dataset consisted of one average IPE for each soil variable at each unique site, paired with a measure of its variance (either the s.d. of the IPE, or, where there was only one comparison, the inverse of sample size, or $1/n$). We also conducted sensitivity analyses to examine robustness of our results to metrics of study precision; more information is included in Methods in the electronic supplementary material.

(d) Meta-analysis

We performed multi-level mixed effects meta-analyses using the *metafor* package in R [19] to examine how effect sizes varied with climate, biome, soil chemical variable, land-use history and landscape configuration. In these models, study identity was included as a random effect to control for potential non-independence of effect size estimates originating from the same publication. All models were fitted using maximum-likelihood estimation [20], and the significance of moderator variables (i.e. fixed effects) was evaluated using Wald-type tests [19,21]. Back-transformed effect sizes within each subgroup, expressed as mean percentage difference in soil properties between Trt_A and Trt_B, are reported in electronic supplementary material, table S2.

We used several methods to assess potential publication bias (over-estimation of effect sizes owing to 'missing' data points that were not published due to negative or null results). First, we used the trim and fill method [22] to estimate the number of 'missing' or unpublished studies in the overall dataset. This was accomplished using the *trimfill* function in *metafor*, which automatically performs the Egger's regression test [23] for funnel plot asymmetry. To quantify the robustness of our results, we re-calculated the overall effect size and its confidence interval using the methods of Henmi & Copas [24], which yield more conservative effect size estimates in the presence of publication bias.

3. Results

The 108 studies included in our meta-analysis yielded 1030 log response ratios. The dataset represents all continents except Antarctica and spans broad gradients of climate (MAP: 52–5000 mm yr^{-1}, MAT: −2.0 to 27.9°C) and latitude (−39.95 to 67.02). Across the entire dataset, the mean IPE (0.343, 95% CI: 0.284–0.402) was highly significant, corresponding to an average 40.9% difference in soil properties among different plant treatments. Across the entire dataset (all 1030 observations), both MAT ($p = 0.003$) and absolute latitude ($p = 0.013$) exhibited weak negative relationships with IPEs (figure 2). Mean annual precipitation was not a significant predictor of effect size. Altogether, MAP, MAT and latitude explained less than 20% of the variance in effect sizes across the dataset (likelihood ratio test pseudo-$R^2 = 0.169$).
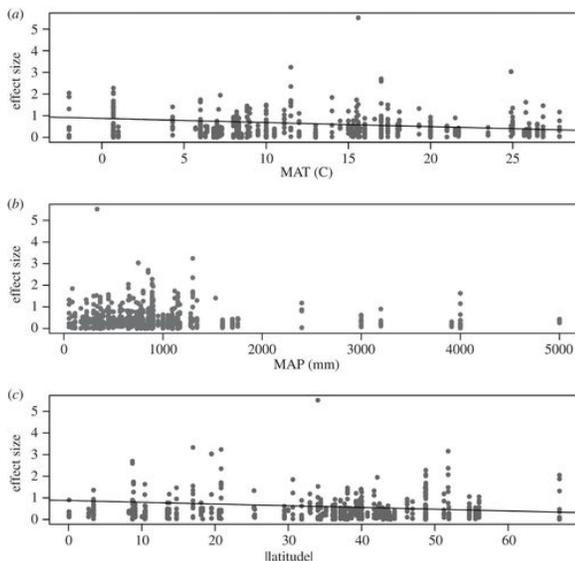

Figure 2. IPEs plotted as a function of (*a*) mean annual temperature, (*b*) mean annual precipitation and (*c*) latitude (absolute value) across the entire dataset. Significant regression slopes and intercepts are shown in panels (*a*) and (*c*).

Mean IPEs were 21% greater in organic versus mineral horizons (Wald test statistic Q_M = 132.4, $p < 0.001$), and varied according to focal soil variable (Q_M = 269.3, $p < 0.001$; figure 3 and **table 1**). The largest effects were observed for base saturation, electrical conductivity and plant-available Ca, N, P and Zn. Plant effects on exchangeable sulfur, soil bulk density and soil moisture were not significant, as 95% CIs overlapped zero.
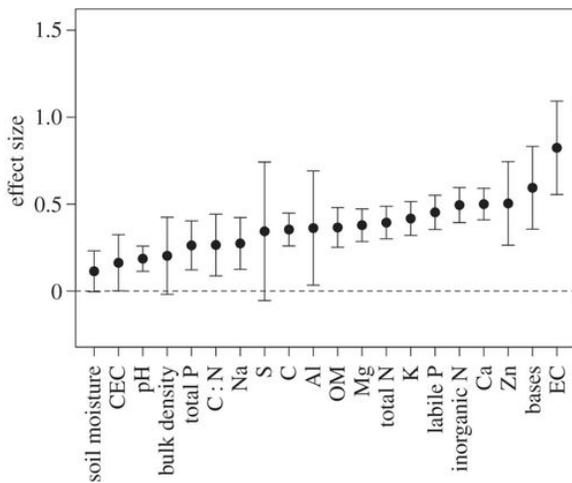

Figure 3. IPEs as a function of soil properties. Error bars are 95% CIs.

Biome type influenced the magnitude of IPEs (Q_M = 131.5, $p < 0.001$); in general, plant effects on soil heterogeneity were 10–30% smaller in forests and grasslands versus tundra and desert (figure 4a). IPEs were strongest for plants growing in a mineral soil matrix, and weaker when individual plants were surrounded by grass, shrubs or trees (Q_M = 131.3, $p < 0.001$, figure 4b). Land-use history had a strong impact on plant effect size, with IPEs on average 44% lower in plantations versus primary or naturally regenerating systems (Q_M = 95.0, $p < 0.001$; figure 4c).
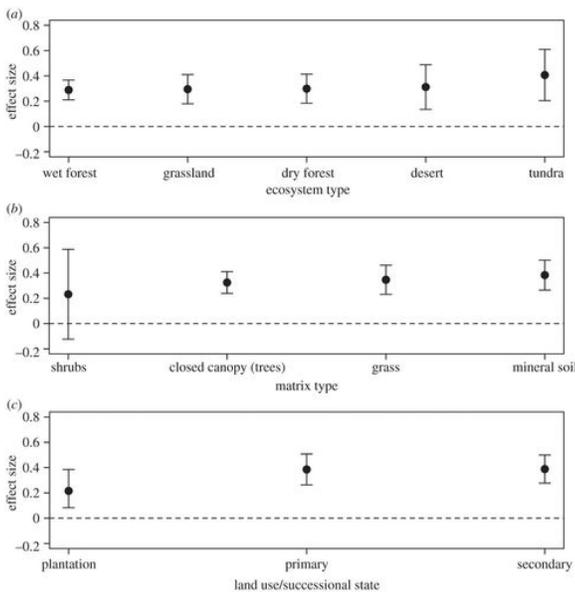

Figure 4. IPEs as a function of (a) ecosystem type, (b) matrix type and (c) land-use history. Error bars are 95% CIs.

(a) Publication bias

The Egger regression test suggested significant asymmetry in the funnel plot of standard errors versus effect size (z = 7.5317, p < 0.0001). This is expected given that the lower bound of our effect size metric was set at zero. However, using the trim-and-fill approach, the number of missing studies in the meta-analysis was estimated at 0 (s.e. = 17.3), suggesting an absence of substantial publication bias (electronic supplementary material, figure S1a). Sensitivity tests [24] revealed that the overall effect size estimate was robust to inclusion of potentially missing studies (re-calculated mean effect size = 0.2847; 95% CI: 0.2340–0.3353).

4. Discussion

Our comprehensive literature survey reveals that plant effects on soil properties are pervasive across ecosystems spanning large climatic and biogeographic gradients. These results are consistent with a high degree of soil heterogeneity at the plant canopy scale, regardless of climate or vegetation type. In the following, we discuss our findings in the light of the four hypotheses.

(a) Effects of climate, plant community structure and successional stage on plant-induced soil heterogeneity

The weak relationship between plant effects and abiotic conditions suggests that temperature and precipitation have limited effects on plant–soil relationships, contrary to our first hypothesis. Plant-induced soil heterogeneity was observed at the extremes of climatic variability, from Arctic tundra to tropical forests. However, we did find evidence for a negative relationship between plant effects and MAT, which may reflect slower rates of nutrient cycling (and therefore greater persistence of plant signatures) in colder ecosystems. Surprisingly, after controlling for effects of climate, we found a weak but significant negative correlation between individual plant effects and latitude. Stronger individual plant effects in tropical ecosystems may be related to pronounced interspecific heterogeneity in foliar nutrient content that characterizes many tropical forests [10,25]. Overall, however, temperature, rainfall and latitude explained only a small fraction of the variance in plant effects observed across studies.

We found partial support for our second hypothesis, that biome type (i.e. dominant vegetation) and landscape patchiness (aggregation of individual plants) influence the magnitude of individual plant effects. Effect sizes were greater in deserts and tundra, which encompass cold and/or dry sites where water and temperature limit plant growth. Plant effects also tended to be greater in ecosystems where individual plants are surrounded by mineral soil (i.e. where the distance to the nearest neighbour is large). This result is consistent with the large body of literature on islands of soil fertility beneath shrub canopies in arid ecosystems [26]. However, a somewhat surprising finding is that plant species continued to exert a significant effect on soil chemistry in both wet and dry forests, where soil properties beneath canopies of different species differ by an average of 33% and 35%, respectively. Strong plant effects in forested ecosystems may be attributable to high heterogeneity in foliar chemistry among tree species [27,28]. Moreover, because roots and their associated fungi decay *in situ*, the chemical signature of individual plants may be largely driven by interspecific variation in root tissue chemistry [29]. This hypothesis is consistent with emerging evidence that root-derived compounds comprise a substantial fraction of stable soil organic matter (SOM) [30].

We found evidence that the strength of plant–soil interactions varied according to land-use history, confirming our third hypothesis. Individual plant effects were significantly lower in managed versus unmanaged ecosystems, suggesting that frequent anthropogenic disturbance may decrease effect sizes. Strong effects of plants on surrounding soils have been observed in older, lightly managed tree plantations [14,31]. However, the impact of plant species on soil nutrient dynamics may be disrupted by frequent crop rotations and removal of

litter residues [32], or may simply take a longer time to develop than in the managed systems we included in our analysis.

(b) Plant effects on different soil properties

The data support our final hypothesis that individual plant effects are stronger for essential macronutrients compared with non-essential or potentially toxic elements. In our dataset, plant presence and species identity strongly affected concentrations of plant-essential mineral ions, such as nitrate, ammonium and phosphate. Yet bulk density, soil C : N, and total C, N and P stocks were less affected. Because total nutrient pools are larger and have slower turnover times than labile nutrients, it is not surprising that total nutrient stocks are less sensitive to the presence of plants. The stronger effect sizes for extractable versus total soil nutrients may also suggest a 'microbial bottleneck' that generates a decoupling between plant inputs of labile nutrients and the formation of older, more stable SOM [33]. In other words, whereas plants may influence the distribution of inorganic nutrients in their surrounding soils, microbial biomass stoichiometry and substrate use efficiency determine whether these differences are translated into long-term changes in bulk SOM chemistry [34,35].

In general, plant effects were stronger for macronutrients (N, P, K, Mg, Ca) than for physico-chemical properties such as soil pH, bulk density and moisture content. The relatively strong effect sizes for macronutrients may be caused by the relatively high degree of plant control over the distribution of essential and non-essential elements [15]. In other cases, small effect sizes may reflect inherently low variability of some soil properties. For example, soil pH exhibits a very narrow range, but small changes in pH value have large implications for plant survival and reproduction. Therefore, we emphasize that the absolute values of individual plant effects are not necessarily correlated with the magnitude of ecological effects caused by plant-induced changes in soil chemistry.

(c) Limitations of the dataset

Variation in soil properties influences the distribution of plant species across the landscape; for example, in a comparative study across three hyper-diverse tropical forests, 25–40% of taxa showed significant associations with soil nutrient availability [36]. Therefore, fine-scale heterogeneity in soil properties may be a driver of plant community structure, rather than a consequence of species' spatial arrangement. The studies included in this meta-analysis are observational, making it difficult to determine the direction of causality. Yet several lines of evidence suggest that our results reflect the influence of plants on their surrounding environment, rather than reverse. First, we observed some of the strongest effects when soils were compared under plants versus mineral soil immediately adjacent to the edge of the plant canopy. As demonstrated in Zinke's classic 1962 paper [7], this is consistent with the spatial signature of plant-induced soil heterogeneity. Additionally, effect sizes in plantations, where soil properties were presumably homogenized prior to plant establishment, were significantly different from 0 (although smaller than in unmanaged ecosystems). Finally, the studies included in this meta-analysis were explicitly focused at the plant-canopy scale. Although plant taxa do sort along gradients of nutrient availability, this edaphic variation occurs at larger spatial scales and is often linked to changes in topography or soil parent material [36,37]. However, we emphasize that manipulative studies are needed to disentangle the two-way relationships between plants and their surrounding soils. Because the studies summarized here did not control for plant placement, our results may represent an upper bound on the magnitude of plant-induced soil heterogeneity.

(d) Consequences of plant-induced soil heterogeneity

Our analysis focused solely on the impact of plants on their surrounding soils. However, the strong patterns that we observed in plant-mediated soil heterogeneity may feed back to influence plant growth and, in turn, community composition and ecosystem-scale patterns of element cycling. Such PSFs may drive ecosystem succession and maintain plant community diversity [38,39]. However, the vast majority of PSFs have been

studied in temperate grasslands [8], where plant communities are easier to manipulate. Our results suggest that PSFs may be a ubiquitous feature of grasslands as well as forests, deserts and tundra ecosystems, at least to the extent that PSFs are determined by variation in soil chemistry. PSFs are often maintained via plant effects on plant microbial communities (symbiotic fungi and bacteria, as well as pathogens [39], which we did not examine here). There is some evidence that soil nutrient content can impact community structure of mycorrhizal fungi [40] and nitrogen-fixing bacteria [41] independently of plant host identity. Therefore, when plant-generated soil heterogeneity influences the spatial structure of microbial communities, microbially mediated PSFs may develop.

The strong influence of individual plants on their surrounding soils has implications for the partitioning of carbon and nutrients among plant, soil and atmospheric pools. Multiple studies demonstrate substantial differences in C and N cycling rates among single-species plantations or stands [42,43], but we might expect these effects to be diluted by competition with neighbouring individuals in mixed stands. However, our results demonstrate that interspecific differences in surrounding soils can be maintained at the level of the individual tree canopy, even in extremely diverse ecosystems such as wet tropical forests. Because substantial biogeochemical heterogeneity exists at relatively small spatial scales, local conditions may as important as broader climatic factors for predicting rates of ecosystem processes [44]. Thus, individual plant effects on their surrounding soils may be a vital part of local-scale ecosystem dynamics.

Author contributions

J.S.P., B.G.W. and S.A.S. designed the research. L.A.-C., K.E.B., K.K.B., S.D., M.G.G., A.B.K., O.R.L., L.M., S.M., C.E.R., M.E.R.-R., R.M.S., S.A.S. and J.S.P. collected the data and discussed the concepts. B.G.W. performed statistical analysis. B.G.W. and J.S.P. wrote the manuscript with input from L.A.-C., K.E.B., K.K.B., S.D., M.G.G., A.B.K., O.R.L., L.M., S.M., C.E.R., M.E.R.-R., R.M.S. and S.A.S.

Competing interests

The authors declare no conflicts of interest.

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