The ecological importance of intraspecific variation

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Human activity is causing wild populations to experience rapid trait change and local extirpation. The resulting effects on intraspecific variation could have substantial consequences for ecological processes and ecosystem services. Although researchers have long acknowledged that variation among species influences the surrounding environment, only recently has evidence accumulated for the ecological importance of variation within species. We conducted a meta-analysis comparing the ecological effects of variation within a species (intraspecific effects) with the effects of replacement or removal of that species (species effects). We evaluated direct and indirect ecological responses, including changes in abundance (or biomass), rates of ecological processes and changes in community composition. Our results show that intraspecific effects are often comparable to, and sometimes stronger than, species effects. Species effects tend to be larger for direct ecological responses (for example, through consumption), whereas intraspecific effects and species effects tend to be similar for indirect responses (for example, through trophic cascades). Intraspecific effects are especially strong when indirect interactions alter community composition. Our results summarize data from the first generation of studies examining the relative ecological effects of intraspecific variation. Our conclusions can help inform the design of future experiments and the formulation of strategies to quantify and conserve biodiversity.

Ecologists have long studied how organisms affect their environments. Early research focused on the ecological effects of keystone, invasive, foundation and dominant species[1–3]. The results of experiments in which focal species were removed or replaced with another species prompted the discovery that certain species strongly influence community structure and ecosystem function[1,2]. Subsequent research largely focused on diversity at the species level. Specifically, a species' ecological effects are determined by experiments that manipulate its incidence and abundance. More recently, research has broadened the characterization of diversity to incorporate the considerable phenotypic and genotypic variation within and among populations of single species[4], including those undergoing contemporary (rapid) evolution[5–10]. Studies have demonstrated that phenotypic trait variation within species (intraspecific variation) can be as extreme as the trait variation across species[11]. As a result, intraspecific variation may influence community structure and ecosystem function as much as variation among species[12–16].

Recent studies in various systems have established the ecological effects of intraspecific variation. For example, variation in consumer foraging traits (such as gill raker size and spacing in fish) can affect zooplankton abundance directly through consumption and phytoplankton primary productivity indirectly through trophic cascades[12,13]. Similarly, variation in anti-herbivory traits (for example, plant chemical defenses) can directly affect arthropod community composition and indirectly affect nutrient cycling via decomposition[17,18]. Yet, researchers have not broadly quantified the general ecological importance of intraspecific variation relative to species variation, leaving open the question, 'Can the ecological responses to phenotypic trait variation across species be extended to intraspecific trait variation within species?' We address this question by conducting a meta-analysis of experimental studies to determine the relative ecological importance of intraspecific variation (replacement of one genotype, phenotype or ecotype with another) compared with the effects of species presence (removal or replacement with another species).

Understanding the ecological effects of intraspecific variation is important for models predicting the consequences of biodiversity loss and rapid trait change[19,20]. Currently, conservation efforts generally focus on species, especially those with large ecological effects and significant contributions to ecosystem services[2,21]. However, conservation efforts that target species diversity may overlook intraspecific variation and its corresponding ecological effects[22]. Intraspecific variation is particularly subject to human impacts through selection and local extirpation[7,20,23]. For example, recent studies have reported massive current and projected declines in population genetic diversity[24]. Thus, a thorough understanding of the ecological effects of intraspecific variation will be critical for predicting how rapid, widespread changes in biodiversity within species will impact communities and ecosystems[25].

In nature, the generation of intraspecific variation can occur through a variety of mechanisms, including local adaptation, artificial selection, parental conditions and phenotypic plasticity[4]. When generated by evolutionary mechanisms, intraspecific trait variation can reflect microgeographic adaptation, divergent selection and even incipient speciation[26]. When generated by plasticity, traits can change rapidly within generations and differ drastically across populations in dissimilar habitats[27]. Regardless of the mechanistic underpinnings, it is the phenotypic manifestation of this variation

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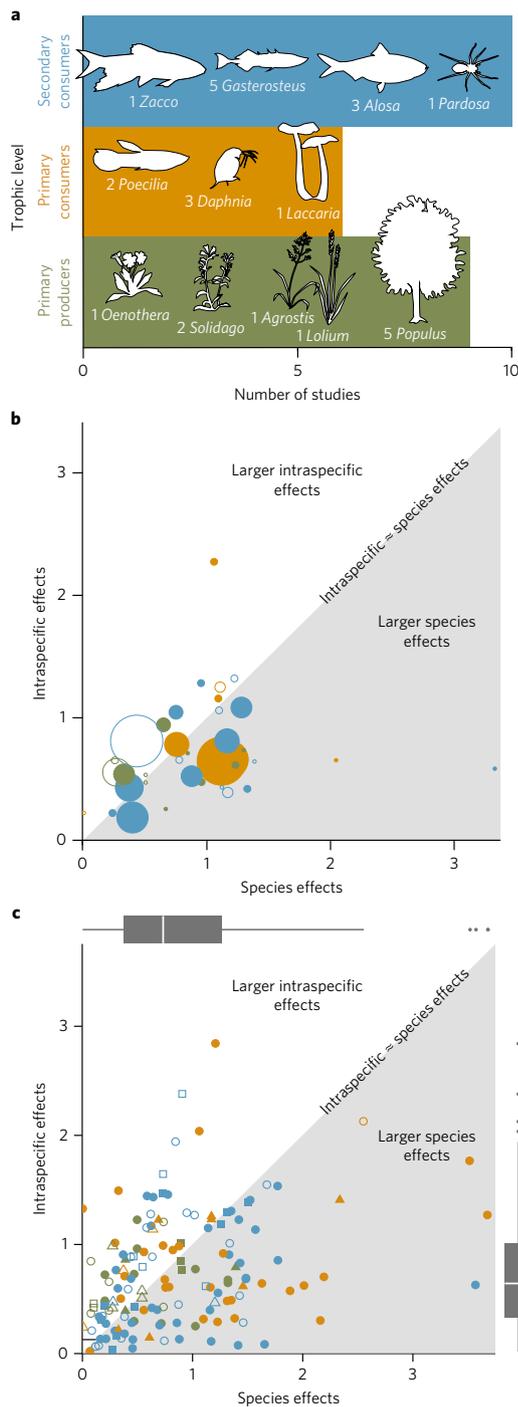
Fig. 1 | Summary of studies used in the meta-analysis and the standardized intraspecific and species ecological effects. a, Focal species grouped by trophic level and showing the number of independent experiments. Focal species were placed in the lowest trophic level that they occupy. **b**, Standardized (mean and standard deviation) intraspecific versus species effects for each study with colour representing the trophic level, point size representing the number of responses measured and fill representing direct (filled) and indirect (unfilled) ecological effects. Points falling in the top left half of the graph represent larger intraspecific effects, while points falling on the bottom right represent larger species effects. **c**, Intraspecific versus species effects for all response variables with colour representing the trophic level, fill representing the direct (filled) and indirect (unfilled) ecological effects and shapes representing whether the response is a change in abundance (circle), process (triangle) or composition (square). Box plots show the interquartile range of the data.

that generates ecological impacts[28]. As a result, we included studies that examine the ecological effects of intraspecific variation in life history (for example, Palkovacs and Post[12]), ecotype (for example, Des Roches et al.[29]), genotype (for example, Chislock et al.[30]), behaviour (for example, Royauté and Pruitt[31]) and previous environmental exposure (for example, Bowatte et al.[32]) in our meta-analysis. By assessing the relative importance of intraspecific versus species effects, our meta-analysis establishes the broader ecological consequences of human-driven evolution, phenotypic plasticity and population extirpation[20,33].

We calculate the importance of intraspecific effects relative to species effects in various study systems. Many recent studies examine intraspecific effects in numerous species and ecosystems (for example, walkingstick insects[34], salamanders[35] and copepods[36]); however, to compare intraspecific effects against species effects, we limit our meta-analysis to experiments that also measured the overall ecological responses to species presence (that is, removal or replacement with another species). We include studies that targeted different focal species at different trophic levels in different habitats (Fig. 1a). Our analysis generalizes across diverse response variables, such as population abundance, rates of ecological processes and community composition at different trophic levels. In addition, we incorporate both direct (consumption or excretion) and indirect interactions (mediated through another organism or nutrient[37]). We predict that ecological effects of phenotypic trait variation across species can be extended to trait variation within species. Therefore, we expect intraspecific effects to be similar in magnitude to species effects across a range of ecological response variables.

Results

Estimation of Hedges' g. Our results summarize data from 25 different studies, which together focus on 12 genera at 3 trophic levels (Fig. 1a and Supplementary Fig. 1). Our results show species effects to be 0.39 standard deviations (s.d.) larger than intraspecific effects with confidence intervals (CIs) that do not overlap zero (Hedges' $g \pm 0.25$ 95% CI, Z-score $= 3.16$, $P = 0.0016$; Fig. 2). Although significant, an effect size slightly above 0.3 demonstrates that the difference between species effects and intraspecific effects is small in magnitude[38]. Of the 146 responses that we include in the analysis, 40% show larger species effects ($g > 0.3$), 35% show similar intraspecific and species effects ($-0.3 \leq g \leq 0.3$) and 25% show larger intraspecific effects ($g < -0.3$). When we estimated the average effect size by study, 56% of the 25 studies showed larger species effects ($g > 0.3$), 36% showed similar intraspecific and species effects ($-0.3 \leq g \geq 0.3$) and 8% showed larger intraspecific effects ($g < -0.3$). Almost half (48%) of the studies examined contain at least one response with a larger ($g < -0.3$) intraspecific effect.

Our base model includes both focal species and study as nested random effects, but only study explains significant variation in the data ($\sigma^2_{species}$ estimate $= 0.00$; σ^2_{study} estimate $= 0.37$), suggesting considerable differences across studies, but not necessarily across focal species (Fig. 2). Estimates of effect size are similar from models with and without focal species included as an effect. Nevertheless, we include focal species as a nested random effect in all downstream models in case it has an important, but undetectable effect.

Effects of study design and response variables. Our final mixed-effects model shows significance in two main effects, but not their interaction: the relationship with the focal species (direct or indirect) and the type of ecological response (abundance, rate or composition). Overall, effect size is significantly higher, thus species effects are stronger, for direct compared with indirect ecological responses ($Z = 3.53$, $P = 0.0004$; Fig. 3). For direct responses, species effects are larger than intraspecific effects (g: 0.43 ± 0.24 95% CI), whereas for indirect responses, intraspecific effects are similar to species effects (g: 0.28 ± 0.25 95% CI). Species effects are
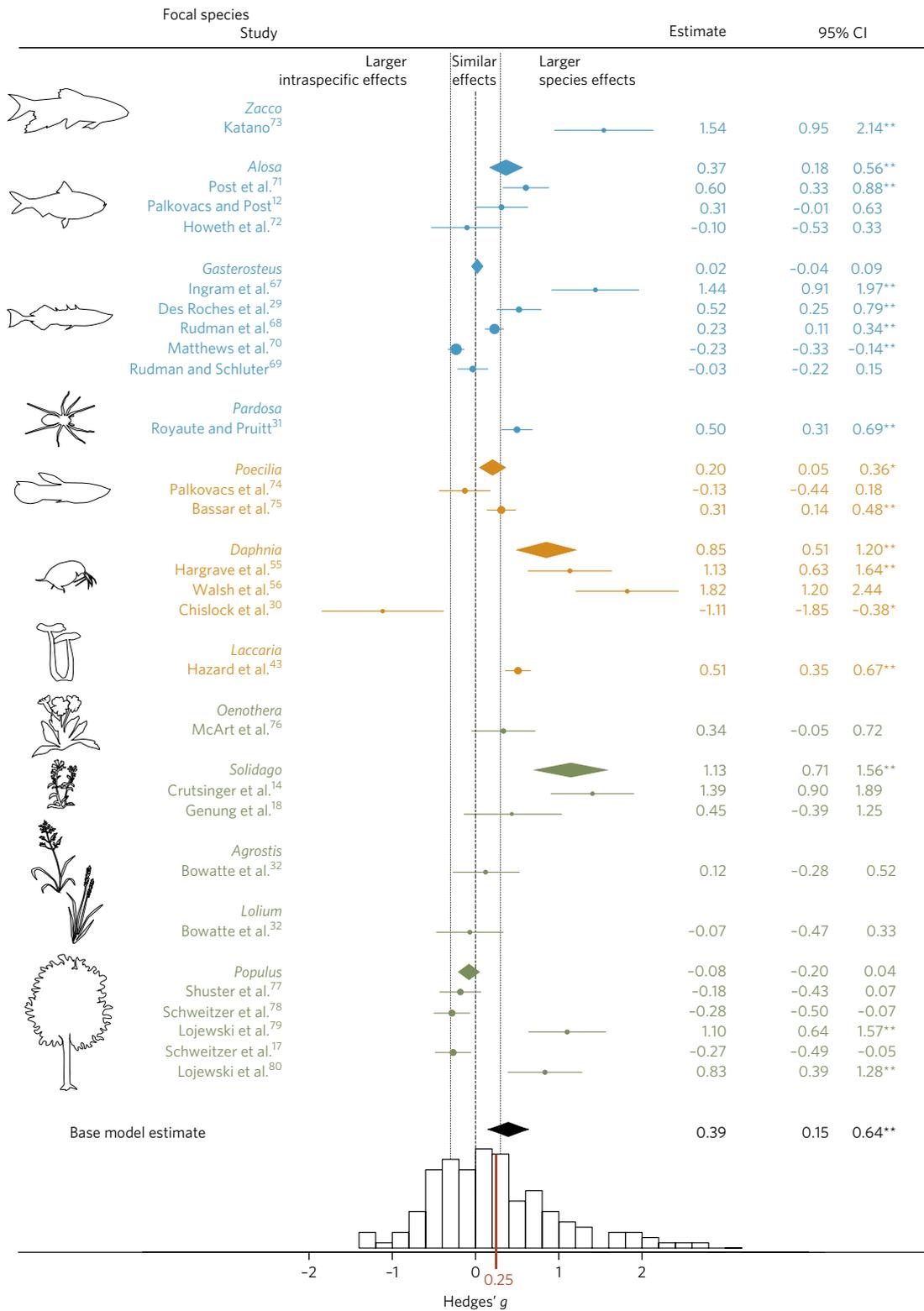
Fig. 2 | Hedges' _g_ values (± 95% CIs) grouped by focal species (polygons) and studies for which intraspecific effects are larger (_g_ < −0.3), similar to (−0.3 < _g_ < 0.3) or smaller than (_g_ > 0.3) species effects. For studies with more than one ecological response, _g_ estimates were derived from a nested random-effects model (species > study). For studies with only one response variable, _g_ was calculated directly. The symbol size corresponds to estimate precision, thus the proportional weight of that study in the model. The distribution of raw _g_ values for all responses is displayed by a histogram at the bottom, with the raw mean shown in red. *$P < 0.01$; **$P < 0.001$.

consistently higher for direct responses compared with indirect responses, regardless of whether they measure changes in abundance ($P = 0.1$), rates of a process ($P = 0.01$) or shifts in community composition ($P < 0.0001$; Fig. 3). Thus, the model including both the relationship with the focal species (direct or indirect) and the type of ecological response (abundance, rate or composition) shows
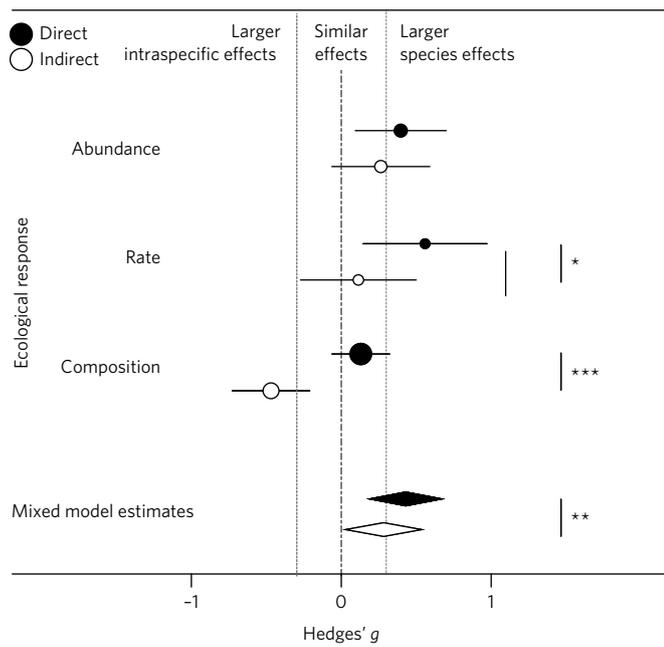
Fig. 3 | Hedges' *g* values (± 95% CIs) grouped by ecological response and the direct (filled) versus indirect (unfilled) effects of the focal species for which intraspecific effects are larger (*g* < −0.3), similar to (−0.3 < *g* < 0.3) or smaller than (*g* > 0.3) species effects. Polygons reflect overall *g* estimates from a mixed-effects model with nested random effects (species > study). Symbol size reflects estimate precision. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

significant main effects ($P < 0.05$), but no significant interactions ($P > 0.05$). Intraspecific effects are comparable to species effects for indirect changes in abundance (*g*: 0.27 ± 0.33 95% CI) and rates of ecological processes (*g*: 0.11 ± 0.38 95% CI), but are larger than species effects for indirect changes in community composition (*g*: -0.47 ± 0.26 95% CI).

Discussion

There is increasing appreciation for the ecological effects of variation within species[6,8,9,16,25,28,39,40]; however, the general importance of such effects compared with species effects is not well resolved. Furthermore, recent work has shown that the ecological effects of different species may be caused in part by intraspecific variation[41]. Disentangling these two sources of variation is difficult because most experiments reporting species effects usually incorporate intraspecific effects only implicitly. As a result, ecological responses can be contingent on the particular variant, population or type used to represent each 'species'. Our meta-analysis disentangles these sources of variation and shows that intraspecific effects on communities and ecosystems can rival the effects of species removal or replacement. For direct interactions, such as consumption, species effects are consistently stronger than intraspecific effects. Yet, for indirect interactions, such as through trophic cascades, species effects are equal to or weaker than intraspecific effects. Intraspecific effects appear to be especially strong when indirect interactions impact compositional responses, such as the cascading effects of predators on the richness of primary producers[42]. Since researchers may more typically measure direct changes in abundance rather than indirect changes in more nuanced ecological responses (such as community composition), the magnitude of intraspecific effects may be even further underestimated.

Intraspecific effects and species effects have roughly similar impacts on most ecological responses (Fig. 1b,c). Specifically, fewer than half of all the responses show stronger species effects and these cases usually reflect direct changes in abundance due to trophic interactions. For example, different freshwater fish species differentially depress the density of their prey through consumption[12,29] and different terrestrial plant species have distinctive effects on the biomass of arthropod consumers[17,18]. Thus, distinct species often cause diverse direct effects due to straightforward exploitative relationships. We would expect, therefore, that replacing the focal species with a congener would have a much smaller ecological effect than removing it completely. Yet, effect size does not differ significantly between replacement and removal experiments, although studies with the strongest species effects are removal studies (Table 1 and Fig. 2). Moreover, effect sizes are similar regardless of whether the focal species is replaced with a congener (for example, Crutsinger et al.[14]) or a distant relative (for example, Hazard et al.[43]). Finally, effect sizes do not differ considerably between studies using intraspecific variants resulting from divergent selection (for example, Des Roches et al.[29]) versus presumed panmictic populations (for example, Royauté and Pruitt[31]). However, we did not have the statistical power to make this comparison.

For indirect ecological responses, the intraspecific and species effects are similar (Fig. 3). In the studies that manipulated secondary consumers (for example, Des Roches et al.[29] and Royauté and Pruitt[31]), indirect responses often occurred via trophic cascades. In contrast, in the studies that manipulated intraspecific variation in primary producers (for example, Schweitzer et al.[17], Chislock et al.[30] and Bowatte et al.[32]), indirect effects occurred via soil and nutrient microbe composition[44], rather than bottom-up trophic effects on predators (but see Ohgushi[45] and Müller et al.[46], which did not meet our criteria for inclusion). A limited set of studies showed that intraspecific effects were even larger than species effects for indirect compositional responses, such as changes in community structure. Intraspecific variation may prompt indirect shifts in compositional responses by altering the nature of interactions (see Bolnick et al.[6]). In freshwater systems in particular, indirect effects can occur through 'cryptic cascades'[42] where fish consumption of zooplankton restructures phytoplankton species composition. For example, anadromous alewife (*Alosa pseudoharengus*) consume more large-bodied zooplankton than landlocked alewife[12]. Release from zooplankton herbivory increases the proportion of edible relative to inedible phytoplankton, thus decreasing the richness but not necessarily the abundance of primary producers[47]. In terrestrial systems, indirect interactions may be mediated by plant–microbial interactions. For example, plant genotypes differentially interact with soil microbes, thus indirectly affecting neighbouring plant diversity[44]. Few studies examined the indirect bottom-up effects of primary producer intraspecific variation on secondary consumer composition; however, some evidence shows that different plant genotypes can affect predator richness through herbivorous arthropods[48].

Although researchers are beginning to study intraspecific effects in a wider range of taxa, there remains an emphasis on species with pronounced ecological impacts or distinctive phenotypic or genotypic variation[34–36]. Thus, we might expect the 75% of studies that focus on keystone species (for example, *A. pseudoharengus*), foundation species (for example, *Populus* species) or strongly divergent populations (for example, *Gasterosteus aculeatus*) to upwardly bias estimates of intraspecific effects. Yet, we found that the intraspecific effects of these species do not differ significantly from the others. Furthermore, effect size estimates from model systems such as *Daphnia* and *Populus* are highly variable within and among studies (Fig. 2). Still, our analysis synthesizes the findings of a relatively new field that is currently dominated by studies of terrestrial vascular plants and freshwater fishes (Fig. 1a). Our results, therefore, form the groundwork for future research on more diverse taxa and

Table 1 | Characteristics of studies (by author) included in our meta-analysis, including focal species, species ('replacement' versus 'removal') and intraspecific treatments, and categorization of all response variables measured as 'direct' or 'indirect' and as 'abundance', 'rate' or 'composition'

Study	Treatments			Response		
	Focal species	Species	Intraspecific	Direct	Indirect	Type
Ingram et al.[67]; Des Roches et al.[29]; Rudman et al.[68]; Rudman and Schluter[69]; Matthews et al.[70]	*Gasterosteus aculeatus* (threespine stickleback)	Removal	Ecotypes or populations	N, PO$_4$, NH$_4$, DOC, DO concentration; benthic invertebrate, zooplankton biomass and number	NO$_3$, phytoplankton and periphyton chlorophyll concentration; rotifer, bacteria number and biomass; light, macrophyte percentage	Abundance
					Decomposition rate	Rate
				Benthic invertebrate, zooplankton richness	Rotifer, phytoplankton, bacteria richness	Composition
Post et al.[71]; Palkovacs and Post[12]; Howeth et al.[72]	*Alosa pseudoharengus* (alewife)	Removal	Life history	Zooplankton length and biomass	Filtered, edible chlorophyll concentration	Abundance
				Zooplankton richness and diversity	Phytoplankton richness and diversity	Composition
Royauté and Pruitt[31]	*Pardosa milvina* (wolf spider)	Removal	Personality	Arthropod prey number		Abundance
Katano[73]	*Zacco platypus* (pale chub)	Removal	Ecotypes	Benthic invertebrate number	Total chlorophyll concentration	Abundance
Palkovacs et al.[74]; Bassar et al.[75]	*Poecillia reticulata* (trinidadian guppy)	Removal	Populations	DO concentration; benthic invertebrates, zooplankton, algae biomass and number	Biomass specific productivity	Abundance
				Algae accrual, PO$_4$ excretion; N, PO$_4$, NH$_4$ flux	Decomposition rate, NO$_3$ flux	Rate
Hargrave et al.[55]; Walsh et al.[56]; Chislock et al.[30]	*Daphnia* species (water flea)	Removal or replacement (congener)	Clones or strains	DO concentration; chlorophyll biomass		Abundance
					Clearance rate	Rate
Hazard et al.[43]	*Laccaria bicolor* (bicolour deceiver mushroom)	Replacement (distant relative)	Genotypes	N, PO$_4$, NH$_4$, DOC, NO$_3$ concentration in soil, shoots and roots; root and shoot productivity		Abundance
McArt et al.[76]	*Oenothera biennis* (primrose)	Replacement (monoculture means)	Genotypes	Arthropod richness		Composition
Crutsinger et al.[14]; Genung et al.[18]	*Solidago altissima* (goldenrod)	Replacement (congener)	Genotypes	Pollinator number		Abundance
					Mass decay	Rate
Bowatte et al.[32]	*Lolium perenne* (ryegrass)	Replacement (distant relative)	Parental conditions		Nitrification	Rate
	Agrostis capillaris (browntop)				Nitrification	Rate
Shuster et al.[77]; Schweitzer et al.[78]; Lojewski et al.[79]; Schweitzer et al.[17]; Lojewski et al.[80]	*Populus* species (cottonwood)	Replacement (congener)	Genotypes	N, C soil percentage; arthropod abundance, biomass production, belowground C allocation	Microbe biomass; C, N, phospholipid fatty acid concentration in microbes	Abundance
				Annual N flux	Annual nitrification	Rate
				Arthropod community composition (NMDS)	Microbe phospholipid fatty acid composition (NMDS)	Composition

DOC, dissolved organic carbon; DO, dissolved oxygen; NMDS, non-metric multidimensional scaling, a measure of community composition.

systems, which will ultimately provide improved insight into the broader ecological role of variation within species. Similarly, better attention to the role of intraspecific variation in studies manipulating species identity and diversity will help us understand the mechanistic links between individuals' traits and their ecological functions[41,44].

Global loss and homogenization of biodiversity are among the most pressing contemporary environmental concerns[22,33]. Motivated by the role of biodiversity in ecosystem function, ecologists and managers typically focus on species as the units of conservation[49]. Although species diversity is clearly important, our meta-analysis reinforces the ecological importance of diversity within species. Not only does intraspecific variation increase demographic resilience and evolutionary potential in populations[50], our analysis shows that it may also structure communities and shape ecosystems[19,22]. Human activity is drastically altering variation within species by driving rapid trait change and extirpation of wild populations[20,33]. Currently, extinction rates of populations are orders of magnitude greater than extinction rates of species[22]. Our results suggest that such rapid and pervasive changes to intraspecific diversity are likely to have important consequences for the future of communities and ecosystems.

Methods

Data selection and collection. We collected data from studies that manipulated the incidence of a focal species (via removal or replacement treatments) and variation within this focal species, whether in genotype, phenotype, ecotype or some combination thereof. As a result, we only used studies that incorporated a treatment where the focal species was either removed entirely or replaced with another species. For example, we excluded the Harmon et al.[13] study on threespine stickleback, which did not estimate a species effect, but we included the related Des Roches et al.[29] study that provided a no fish ('removal') treatment from which to estimate the effect of stickleback presence.

We performed a systematic review of the literature published up to and including September 2016 following TOP[51] (Transparency and Openness Promotion) and PRISMA[52] (Preferred Reporting Items for Meta-Analyses) guidelines (Supplementary Table 1 and Supplementary Fig. 1). We used the Web of Science (Thomson Reuters) and Google Scholar search engines to find studies meeting our criteria. We used a combination of the following terms: ('intraspecific') and ('replacement' or 'removal' or 'interspecific variation' or 'species diversity') and ('top-down' or 'bottom-up' or 'ecosystem effects' or 'community effects'). At least two coauthors independently analysed raw data that were either publicly available (for example, via the Dryad Digital Repository) or provided directly by authors. We excluded only two studies that met our criteria but for which raw data were unavailable (Li et al.[53] and Compson et al.[54]).

Our final dataset included 25 different studies collectively focusing on 12 different genera at various trophic levels (Fig. 1a and Supplementary Fig. 1). Each focal species had between 2 and 23 different variants, collectively representing intraspecific variation (Table 1). Our goal was to emphasize the importance of variation that is often ignored by management efforts that focus on species as the units of conservation. Therefore, we considered intraspecific variation to exist within a conventionally named species (Table 1). The intraspecific treatments in our meta-analysis reflected the authors' original experimental design. In all cases, intraspecific comparisons reflected 'replacement' treatments, where the ecological effects of distinctive intraspecific variants were compared against one another (few studies compare collective intraspecific diversity with species diversity, but see Fridley and Grime[44]). All studies measured at least one ecological response variable and were performed in terrestrial or freshwater habitats in either a natural setting (for example, *Alosa* in entire lakes[12]), semi-natural field enclosures (for example, *Pardosa* in outdoor mesocosms[31]) or regulated laboratory conditions (for example, *Daphnia* in bottles[55,56]).

We first categorized response variables based on whether they were directly or indirectly affected by the focal species (Table 1). When the original authors did not explicitly define or test direct versus indirect effects, we assigned responses based on definitions of 'direct effects' and 'indirect effects' from Strauss[57] and Wootton[37] and knowledge of each study system. Specifically, direct responses involved interactions at the trophic level adjacent to that of the focal species and were usually affected via consumption or excretion. Indirect responses were mediated by another organism or nutrient (for example, via trophic cascade) and involved interactions separated by at least one trophic level[57]. If there was the potential for at least some direct interaction between the focal species and the response variable, we categorized the response as direct. The application of these definitions was based on those of Balvanera et al.[58] and Palkovacs et al.[59] and resulted in unambiguous assignments of responses as either direct effects or indirect effects. We classified response variables as a measurement of 'abundance',

'rate' or 'composition' (Table 1). The 'abundance' category reflected quantities of a single type of organism or nutrient (for example, count, density or concentration). The 'rate' category reflected processes occurring over a unit of time, such as a change in biomass or nutrient concentration (for example, flux, build-up or break-down over time). Finally, the 'composition' category reflected the quantification of a combination of multiple types of organisms (for example, richness, diversity or Bray–Curtis dissimilarity). Categorization of responses as either 'biotic' (for example, population abundance) or 'abiotic' (for example, nutrient concentration) did not significantly affect the statistical outcome and was thus excluded from the final model.

Effect size calculation and analyses. Because researchers recorded different ecological response variables expressed in a variety of units, we used Hedges' g (ref. [60]) as a measure of effect size to compare standardized intraspecific and species effects across studies. For each response variable in each study, we calculated intraspecific effects (μ_{intra}) as the mean absolute value of the pairwise differences in the response variables among the within-species variants. We used the contrast that best reflected the authors' interpretation of the study system, whether it was among different populations, phenotypes or genotypes. We calculated species effects ($\mu_{species}$) as the mean absolute value of the pairwise differences in the response variables between treatments including the focal species (that is, the mean of the intraspecific treatments) and treatments with either the species removed entirely or replaced with a different species. We computed the pooled s.d. (σ_{pooled}) from data used to calculate species and intraspecific means and used the number of replicates as the sample size for each study. We employed the 'escalc' function in the Metafor package (version 2.9-9)[61] implemented in R (version 3.3.2; ref. [47]) to calculate Hedges' g—a bias-corrected version of Cohen's d, as follows:

$$\text{Hedges' } g = \frac{\mu_{species} - \mu_{intra}}{\sigma_{pooled}}$$

Following Cohen[60], effect sizes falling between −0.3 and 0.3 demonstrated relatively equal species and intraspecific effects. Positive values (>0.3) indicated larger species effects. Negative values (<−0.3) indicated larger intraspecific effects.

Statistical models. We used the Metafor 'rma.mv' function[61] using default weighting to test linear random- and mixed-effects models of our data. Our base model specified focal species and study (by publication) as nested random effects (focal species (study)) to account for heterogeneity[62] and non-independence of results[63] from the same study or using the same focal species. We used this base random-effects model to estimate an overall Hedges' g and 95% CIs. We then included attributes of study design and characteristics of the ecological response variables as moderators in two separate mixed-effects models. Aspects of study design that we could consistently determine included habitat (aquatic or terrestrial) and experimental setting (natural, laboratory or field). We also recorded focal species' trophic level (primary producer, primary consumer or secondary consumer) and whether the species treatment was replacement or removal; however, given that all removal studies used consumer species and most replacement studies used producer species, these two moderators were largely confounded. In an additive model, no aspects of study design explained significant variation in the effect size ($P > 0.05$). Our final mixed-effects model therefore only included the following two moderators and their interaction: relationship with the focal species (direct or indirect) and type of ecological response (abundance, rate or composition). We excluded a third response characteristic (trophic level: nutrient, producer or consumer) through model selection (glmulti package version 1.0.7. using the Akaike information criterion[64]). The limited sample size of studies meant that we did not have sufficient degrees of freedom to test the effect of different experimental design moderators on different response variables.

We did not find evidence of publication bias in the studies we surveyed. We minimized the possibility of publication bias of the results within studies by incorporating the original raw data and not just those that were reported. Furthermore, Rosenthal's fail-safe number[65] (3,173) is far greater than the calculated threshold level required for our analysis of $n = 25$ studies ($5n + 10 = 135$). In addition, Egger's regression test[66] ('regtest' function in Metafor) on the relationship between sample size and effect size was not significant for funnel plot asymmetry ($z = -1.16$, $P > 0.05$).

Life Sciences Reporting Summary. Further information on experimental design is available in the Life Sciences Reporting Summary.

Data availability. Data are available through the Dryad Digital Repository (https://doi.org/10.5061/dryad.m5d78).

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Author contributions

All authors developed the study idea and participated in data collection. S.D., D.M.P., N.E.T. and E.P.P. performed the statistical analyses. S.D., D.M.P. and E.P.P. led the writing of the paper. All authors prepared and edited the final drafts.

Competing interests

The authors declare no competing financial interests.

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▶ Experimental design

1. Sample size

Describe how sample size was determined.

Sample sizes reflected the availability of studies that reflected our search criteria. Namely, studies must have: 1) measured at least one ecological parameter, 2) used treatments including different intraspecific variants of the same species, AND 3) used treatments that either removed OR replaced that same focal species.

2. Data exclusions

Describe any data exclusions.

Only two relevant data-sets were excluded as they could not be accessed (original authors did not respond to requests for raw data)

3. Replication

Describe whether the experimental findings were reliably reproduced.

At least two co-authors performed literature searches and data-analysis, for which the findings were consistent.

4. Randomization

Describe how samples/organisms/participants were allocated into experimental groups.

Randomization was not relevant to this study as no experiment was conducted.

5. Blinding

Describe whether the investigators were blinded to group allocation during data collection and/or analysis.

Blinding was not relevant to this study.

Note: all studies involving animals and/or human research participants must disclose whether blinding and randomization were used.

6. Statistical parameters

For all figures and tables that use statistical methods, confirm that the following items are present in relevant figure legends (or in the Methods section if additional space is needed).

n/a	Confirmed	
☐	☒	The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement (animals, litters, cultures, etc.)
☒	☐	A description of how samples were collected, noting whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☒	☐	A statement indicating how many times each experiment was replicated
☐	☒	The statistical test(s) used and whether they are one- or two-sided (note: only common tests should be described solely by name; more complex techniques should be described in the Methods section)
☐	☐	A description of any assumptions or corrections, such as an adjustment for multiple comparisons
☐	☒	The test results (e.g. P values) given as exact values whenever possible and with confidence intervals noted
☐	☒	A clear description of statistics including central tendency (e.g. median, mean) and variation (e.g. standard deviation, interquartile range)
☐	☒	Clearly defined error bars

See the web collection on statistics for biologists for further resources and guidance.

▶ Software

Policy information about availability of computer code

7. Software

Describe the software used to analyze the data in this study.	R version 3.3.1 Metafor package 2.9-9; glmulti package 1.0.7

For manuscripts utilizing custom algorithms or software that are central to the paper but not yet described in the published literature, software must be made available to editors and reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). *Nature Methods* guidance for providing algorithms and software for publication provides further information on this topic.

▶ Materials and reagents

Policy information about availability of materials

8. Materials availability

Indicate whether there are restrictions on availability of unique materials or if these materials are only available for distribution by a for-profit company.	No unique materials were used.

9. Antibodies

Describe the antibodies used and how they were validated for use in the system under study (i.e. assay and species).	No antibodies were used.

10. Eukaryotic cell lines

a. State the source of each eukaryotic cell line used.	No eukaryotic cell lines were used.
b. Describe the method of cell line authentication used.	No eukaryotic cell lines were used.
c. Report whether the cell lines were tested for mycoplasma contamination.	No eukaryotic cell lines were used.
d. If any of the cell lines used are listed in the database of commonly misidentified cell lines maintained by ICLAC, provide a scientific rationale for their use.	No commonly misidentified cell lines were used.

▶ Animals and human research participants

Policy information about studies involving animals; when reporting animal research, follow the ARRIVE guidelines

11. Description of research animals

Provide details on animals and/or animal-derived materials used in the study.	No animals were used.

Policy information about studies involving human research participants

12. Description of human research participants

Describe the covariate-relevant population characteristics of the human research participants.	The study did not involve human research participants.