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A MECHANISTIC UNDERSTANDING OF GLOBAL CHANGE ECOLOGY

The relative importance of plant intraspecific diversity in structuring arthropod communities: A meta-analysis

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Abstract

1. Understanding how plant diversity influences higher trophic levels is important for predicting the consequences of global biodiversity loss. While early studies have focused on the effects of plant species richness, more recently a growing number of experiments have explored the effects of plant intraspecific diversity by manipulating the genotypic richness of plant communities.
2. By combining 162 estimates of effect size from 60 experimental studies, we examined the effects of plant genotypic richness on arthropods, one of the most diverse and abundant taxa which play a crucial role in many ecosystem processes and services. We have also compared the effects of plant genetic and species diversity on arthropods when both were manipulated within the same study.
3. Species richness and abundance of most trophic groups of arthropods were higher in genetically diverse plant stands. Interestingly, the effects of plant genetic diversity on natural enemies of herbivores were stronger than the effects of plant genetic diversity on herbivores, suggesting that plant genetic diversity effects on predators might be driven by mechanisms independent of herbivores.
4. Herbivore and predator abundance increased with plant genetic diversity in studies using wild plants whereas predator abundance was unaffected and herbivore abundance was reduced by crop genetic diversity. Damage by generalist herbivores was reduced by plant genetic diversity whereas damage by specialist herbivores was not affected.
5. When the effects of plant genetic and species diversity on arthropods were compared within the same study, the magnitude of plant genetic diversity effects was comparable to that of plant species diversity.
6. Our results suggest that plant genetic diversity has significant effects on the diversity of arthropods across several trophic levels, thus highlighting the importance of maintaining high levels of both plant species and genetic diversity for arthropod conservation. However, the potential of using crop genetic mixtures in agriculture for pest control appears to be limited as even though herbivore abundance was reduced in genetically diverse plots, herbivore damage and predator abundance were not affected by crop genotypic richness.

KEYWORDS
associational resistance, biodiversity, community genetics, genetic diversity, herbivory, natural enemies, plant–insect interactions, tritrophic interactions

1 | INTRODUCTION

The rapid loss of biodiversity due to human activities and its potential implications for ecosystem functioning, services and human well-being have prompted active research on the relationship between biodiversity and ecosystem functioning (BEF) during the last 20 years. The majority of early BEF studies have been focused on the effects of species loss, which is just one aspect of the multidimensional biodiversity concept. Yet, human activities resulting in land-use change and habitat fragmentation are known to have dramatic effects not just on species diversity but also on intraspecific genetic variation (Mimura et al., 2017) and changes in species richness often occur in parallel with changes in intraspecific genetic diversity and may be causally connected (Vellend & Geber, 2005). For instance, losses in genetic diversity due to shrinking population sizes may precede a loss of species from the community. In a more applied context, crop fields and forest plantations represent plant communities impoverished both in terms of inter- and intraspecific diversity as they are usually dominated by plant monocultures composed of a single cultivar or variety (Tooker & Frank, 2012). Recent studies have shown that plant genetic diversity can be important for ecosystem functioning and in some cases its effects are comparable in magnitude to the effects of species diversity (Crutsinger et al., 2006; Hughes, Inouye, Johnson, Underwood, & Vellend, 2008). Moreover, plant genetic diversity may modify the responses of communities and ecosystems to natural disturbance and anthropogenic environmental change (Hughes & Stachowicz, 2004; Reusch, Ehlers, Hämmerli, & Worm, 2005) and reduce the loss of species diversity (Booth & Grime, 2003). Hence, understanding of the ecological effects of genetic diversity will allow us to anticipate shifts in community structure and function (Whitlock, 2014) and is critically important for conservation and restoration efforts (Kettenring, Mercer, Reinhardt Adams, & Hines, 2014).

Intraspecific genetic diversity can be defined, measured and manipulated in many different ways (Hughes et al., 2008; Whitlock, 2014). One way to study the effects of plant diversity on associated communities of consumers is by experimentally manipulating plant genotypic diversity (i.e. number of genotypes in a population) and examining the resulting changes in abundance and diversity of associated organisms at different trophic levels. While early experiments exploring the effects of plant diversity on arthropods mainly manipulated plant species richness (Koricheva, Mulder, Schmid, Joshi, & Huss-Danell, 2000; Siemann, Tilman, Haarstad, & Ritchie, 1998), a new generation of ecological experiments conducted during the last decade manipulated plant intraspecific diversity (Crutsinger et al., 2006; Johnson, Lajeunesse, & Agrawal, 2006), most recently in combination with plant species diversity (Abdala-Roberts et al., 2015; Cook-Patton, McArt, Parachnowitsch, Thaler, & Agrawal, 2011; Crawford & Rudgers, 2013). A meta-analysis of plant genetic diversity experiments by Bailey et al. (2009) revealed that arthropods showed a stronger response to increases in plant genotypic diversity compared to plants and microbes. However, this analysis was based on results of only 11 experiments available at that time, assessed the absolute magnitude but not direction of the effects of plant genetic diversity on arthropods, and did not compare effects on different trophic levels of arthropods. A more recent meta-analysis of plant genetic diversity experiments by Whitlock (2014) demonstrated that community-level effects of plant genotypic diversity are significant and positive when responses were measured at a different trophic level than the focal plant species, but did not distinguish between responses of different taxa and trophic levels (e.g. primary and secondary consumers).

While ecologists only started to experimentally manipulate plant genotypic richness a decade ago (but see Schmitt & Antonovics, 1986), in agriculture mixing different crop cultivars as a way to manage pests has been attempted since the mid 1980s (Altieri & Schmidt, 1987; Cantelo & Sanford, 1984). This research was partly inspired by the successful use of crop genotypic diversity to reduce damage by fungal pathogens (Mundt, 2002; Zhu et al., 2000) as well as the desire to replicate the success of pest control provided by intercropping (planting mixtures of different crop species) without the associated logistical and financial constraints (Tooker & Frank, 2012). Similarly to ecological experiments, a number of studies in agriculture compared the effectiveness of intercropping with that of crop cultivar or varietal mixtures (e.g. Gold, Altieri, & Bellotti, 1989, 1990; Letourneau, 1995), thus providing comparative data on the effects of crop species and genetic diversity on arthropods. While a recent narrative review by Tooker and Frank (2012) has discussed multiple lines of evidence suggesting that crop genetic diversity can improve pest control in agriculture, a formal quantitative review of the effects of crop genetic diversity on agricultural pests has not been yet conducted.

Understanding the effects of losses of plant genetic diversity on community structure and ecosystem functioning requires exploration of diversity effects across trophic levels. If changes in plant diversity trigger losses of species richness and abundance of associated organisms at other trophic levels, this may seriously impair ecosystem processes and services (Soliveres et al., 2016). A recent narrative review by Moreira, Abdala-Roberts, Rasmann, Castagneyrol, and Mooney (2016) has revealed a number of knowledge gaps in our understanding of plant diversity effects on higher trophic levels. Specifically, it highlighted the need to understand the relative importance of plant intra- vs. interspecific diversity, to include herbivore traits mediating plant diversity effects (e.g. diet breadth), and to investigate the interactions between plant diversity and diversity at higher trophic levels (e.g. predators and parasitoids). Also, while earlier meta-analyses on plant diversity effects often did not distinguish between herbivore responses in terms of abundance and damage (Castagneyrol, Jactel, Vacher, Brockerhoff, & Koricheva, 2014; Jactel & Brockerhoff, 2007), a recent meta-analysis of tree species diversity effects on herbivores by Kambach, Kühn, Castagneyrol, and Bruelheide (2016) has revealed that herbivore abundance, species richness and damage may be differently affected by plant diversity and it is important to distinguish between these response variables.

In this review, we address the above knowledge gaps by conducting a meta-analysis of studies which have explored the effects of plant genotypic richness on associated communities of arthropods. We are focusing on arthropods because they represent one of the most diverse and abundant animal taxa and are ecologically and economically important as they play crucial roles in many ecosystem processes and services (herbivory, pollination, decomposition, predation, parasitism etc.). Specifically, we address the following questions:

1. How does plant genetic diversity affect various trophic groups of arthropods? Do plant genetic diversity effects tend to dampen when moving up a food web?
2. Does plant genetic diversity affect arthropod species richness, abundance and activity differently?
3. Do the effects of plant genetic diversity on herbivores depend on herbivore diet breadth (specialists vs. generalists)?
4. Does plant genetic diversity have a similar impact on arthropods in agricultural and natural ecosystems? Can it be used as a viable pest management strategy in agriculture?
5. How does the magnitude and direction of plant intraspecific diversity effects on arthropods compare with that of plant species diversity effects?

2 | MATERIALS AND METHODS

2.1 | Literature search, inclusion criteria and data extraction

We searched for relevant literature using keyword searches in Web of Science and Google Scholar, reference lists of recent reviews on the topic (Bailey et al., 2009; Tooker & Frank, 2012; Whitlock, 2014) and reference lists of the obtained relevant studies on the topic. Combinations of the following keywords were used: "genetic diversity," "genotypic diversity," "varietal mixtures," "plant," "arthropod," "herbivore," "predator," "parasitoid," "omnivore," "pollinator" and "detritivore."

To be included in our meta-analysis, a study had to satisfy the following inclusion criteria: (1) plant genotypic richness was experimentally manipulated in such a way that replicated low and high genotypic diversity plant stands were available; (2) some measures of arthropod diversity (species richness, Shannon–Weiner index, evenness), abundance, performance (fecundity, biomass) or activity (e.g. herbivory, parasitism rates) were available; (3) data on means, *SD* and sample sizes for the above variables from low and high genotypic diversity treatments were available from the papers or provided by the authors. Behavioural responses such as arthropod movement were not included. Our final database included data from 60 studies published between 1984 and 2017. A list of data sources used in the study is provided in the Data sources for meta-analysis section.

As the aim of the meta-analysis was to compare the effects of plant genetic diversity on different trophic groups of arthropods and on different response variables, we have extracted data for all types of arthropods and all response variables available in each study. The following groups of arthropods were distinguished based on the information provided in the primary studies: total arthropods, herbivores, predators, parasitoids, omnivores and detritivores. The following response variables were included: species richness, Shannon–Weiner diversity index, evenness, abundance, herbivore damage, parasitism rate, fecundity and biomass.

When arthropod responses in a study were measured repeatedly over several sampling dates, we averaged data across the dates before calculating the effect size. While this reduced non-independence of the data, it might have resulted in more conservative estimates of the effect size if effects of genetic diversity increase with time. When different proportions of genotypes in mixtures were tested within the same study, we always chose the mixture containing as equal a proportion of different genotypes as possible. When different spatial arrangements of genotypes in mixtures were tested in the same study (e.g. regular, alternate rows, random), we have always chosen random mixtures if available. When arthropod responses were measured on individual genotypes in the mixture rather than per plot, these genotype-specific responses were averaged across genotypes before calculating the effect size. When treatments other than genetic diversity were used in a factorial experimental design (e.g. application of fertilizers or different levels of plant density), effects of low and high genetic diversity were compared at the lowest levels of other treatments (e.g. no fertilizers, low plant density). WebPlotDigitizer software (https://automeris.io/WebPlotDigitizer) was used to extract the data from figures.

In the majority of studies (43 out of 60), only two levels of plant genetic diversity were used in the experiments. To reduce non-independence due to multiple estimates of effects from the same experiment, we extracted the data only for the lowest and highest diversity levels if a study reported results for >2 levels of genetic diversity.

In 16 out of 60 studies, comparable data on arthropod diversity, abundance, performance or activity in plant monocultures and species mixtures were available in addition to intraspecific genetic mixtures. We have included data from these papers to compare the magnitude and direction of plant genetic and species diversity effects on arthropods.

2.2 | Meta-analysis

Meta-analysis was conducted using OpenMEE software (Wallace et al., 2017). Standardized mean difference (Hedges' *d*) between measures of arthropod abundance, diversity or activity in genetically diverse and genetically poor monospecific plant stands was used as an effect size (Hedges, 1981). This metric of effect size was chosen because it has been used in a number of previous meta-analyses assessing the effects of plant diversity (Jactel & Brockerhoff, 2007; Letourneau et al., 2011; Whitlock, 2014), hence making the results of our analysis comparable with those from earlier studies. A positive effect size indicated higher arthropod abundance, diversity or activity in genetically diverse stands as compared to genetically poor stands. Effect sizes for studies reporting effects of plant species diversity on arthropods were calculated in the same way, i.e. as a standardized mean difference between arthropod response variables in plant species mixtures and monocultures.

Random-effects models were used to combine the effect sizes across studies. These models account for both sampling variance within studies and between-study variance. A restricted maximum likelihood approach was used to estimate the parameters of the meta-analysis model. The mean effect size was considered significantly different from 0 if its 95% CI did not include 0. Total heterogeneity in effect sizes was calculated (Q_t) as well as the proportion of heterogeneity due to between-study variance (I^2). Meta-regression was used to assess the effects of moderators (covariates) on the magnitude of the effect of plant genetic diversity. The moderators considered were different trophic groups of arthropods (total arthropods, herbivores, predators, parasitoids, omnivores and detritivores), arthropod response variables (tested separately within each trophic group), type of plant (crop vs. non-crop), and feeding specialization of herbivore (generalist vs. specialist). Herbivores were considered as specialists if their host plants were restricted to a single genus and as generalists if their host plants belonged to more than one genus. Moderators were tested hierarchically in order to avoid confounding between them, with trophic levels tested first, followed by comparisons of different response variables within each trophic level, and finally type of plant and feeding specialization within each trophic group and response variable. Q_m statistics representing the dispersion explained by the covariates included in the model was used to interpret the significance of the moderators tested.

Responses of different trophic levels of arthropods to plant genetic diversity may be non-independent from each other (e.g. decrease in herbivore abundance and damage in mixed stands may be due to increased abundance and activity of natural enemies). In order to examine possible relationships between responses of different trophic levels of arthropods to plant genetic diversity, we estimated Pearson's correlation coefficient between effect sizes of herbivores and their natural enemies. This analysis was restricted to studies which examined responses of both herbivores and their natural enemies to plant genetic diversity within the same experiment.

To test for possible publication bias, we used funnel plots which represent scatterplots of effect sizes against standard error. A publication bias creates an asymmetric funnel with small studies with non-significant effects missing from the side of the funnel opposite to the true effect. However, asymmetry of funnel plots can be caused by factors other than publication bias, and therefore they need to be interpreted with caution (Lau, Ioannidis, Terrin, Schmid, & Olkin, 2006). Therefore, as an additional approach to assess the potential impact of possible publication bias on our findings, we calculated fail-safe numbers for significant effects using Rosenberg's weighted method (Rosenberg, 2005). Rosenberg's fail-safe number indicates how many additional studies with effect size of 0 and of the same weight as the average of those already being used would need to exist to reduce the significance of the mean effect to 0.05. If the fail-safe number is large (i.e. greater than 5k + 10, where k=number of studies already in the meta-analysis), the results of the meta-analysis are considered robust to possible publication bias.

3 | RESULTS

Our meta-analysis of plant genetic diversity effects on arthropods was based on 60 published studies which yielded 162 comparisons of arthropod diversity, abundance and activity in genetically diverse and genetically poor plant stands. Herbivores were by far the most studied group of arthropods (97 comparisons, 60% of all effect sizes). Omnivores and detritivores were the least studied groups (3 and 2 comparisons, respectively). In some studies, arthropods were not sorted to trophic groups with results reported as total arthropod species richness or abundance (25 comparisons). Genotypic diversity experiments in reviewed studies were performed on over 40 different plant species ranging from annual plants to trees.

Overall, plant genetic diversity had a significant positive effect on arthropods (d = 0.192, 95% CI 0.096 to 0.287, N = 162). While the magnitude of the effect was relatively small, it was robust to possible publication bias, as indicated by the large fail-safe number (N_{fs} = 2,806). Total heterogeneity in the overall model was very high (Q_t = 449.7, df = 161, p < .001) with 67.4% of the observed variance due to differences among studies, thus further exploratory analyses of the moderators were warranted.

Plant genetic diversity effects significantly differed between trophic groups of arthropods (Q_m = 15.875, df = 5, p = .007), which was largely due to differences in responses of herbivores and other arthropods. While herbivores showed no significant response overall, all other trophic groups have been significantly positively affected by plant genetic diversity (Figure 1). Fail-safe numbers indicate that our results for total arthropods and predators are robust to possible publication bias whereas results for parasitoids, omnivores and detritivores have to be interpreted with caution as they are based on a small number of studies and N_{fs} are low (Figure 1). Examination of funnel plots for the individual arthropod groups (see Figures S1–S4) revealed no obvious asymmetry for total arthropods, herbivores and predators, whereas for parasitoids studies reporting negative effects tended to have much larger standard errors than studies reporting positive effects. This asymmetry of the funnel plot is unlikely to be caused by publication bias and appears instead to be due to the fact that studies reporting parasitism rate (which tended to show more negative effects) had lower sample sizes (and thence larger standard errors) than studies reporting parasitoid abundance and species richness (Figure 2).

Both total arthropod abundance and species richness were higher in more genetically diverse stands (abundance: d = 0.424, 95% CI 0.016 to 0.832, N = 7, N_{fs} = 16; species richness: d = 0.626, 95% CI 0.272 to 0.980, N = 12, N_{fs} = 512) while Shannon–Weiner diversity and evenness of arthropods were not significantly affected (Shannon–Weiner index: d = 0.405, 95% CI −0.553 to 1.362, N = 4; evenness: d = −0.047, 95% CI −0.833 to 0.783, N = 2; Q_m = 2.868,

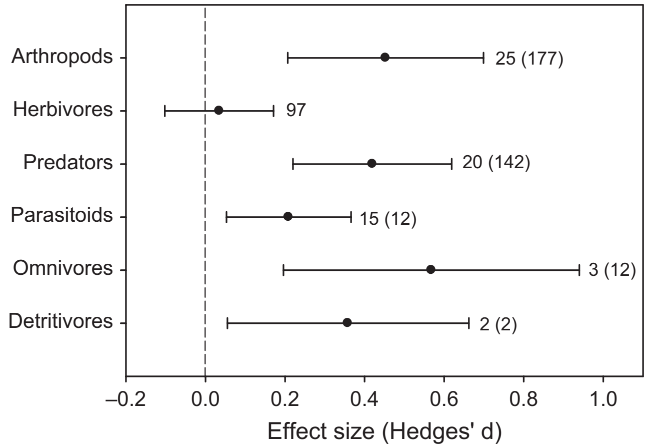

FIGURE 1 Effects of plant genetic diversity on different trophic groups of arthropods. Error bars represent 95% CI. Numbers next to error bars indicate number of studies in each category. Numbers in parentheses are Rosenberg's fail-safe numbers which indicate how many additional studies with effect size of 0 and of the same weight as the average of those already being used would need to exist to reduce the significance of the mean effect to 0.05. Effects are considered significantly different from 0 if 95% CI do not cross 0 (dashed line)

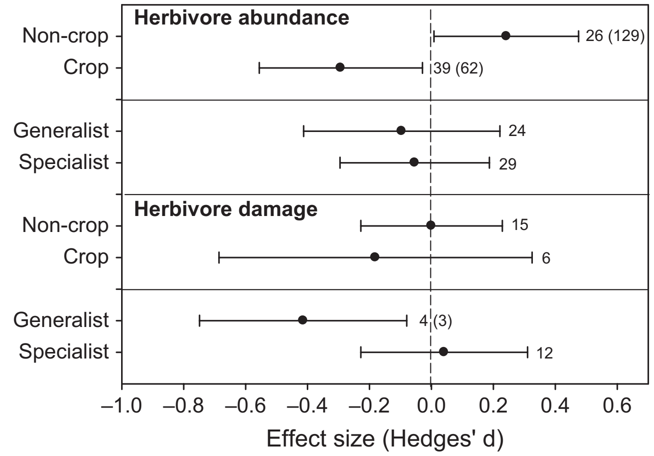

FIGURE 3 Comparison of the effects of plant genetic diversity on herbivore abundance and damage on crops and wild plant species, and for generalist and specialist herbivores. Error bars represent 95% CI. Numbers next to error bars indicate number of studies for each trophic groups. Numbers in parentheses are Rosenberg's fail-safe numbers which indicate how many additional studies with effect size of 0 and of the same weight as the average of those already being used would need to exist to reduce the significance of the mean effect to 0.05. Effects are considered significantly different from 0 if 95% CI do not cross 0 (dashed line)

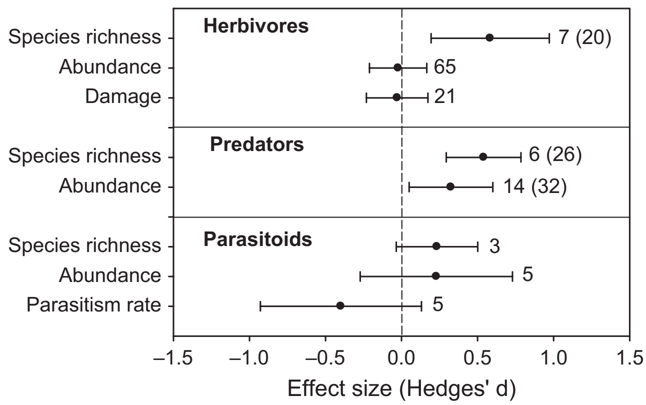

FIGURE 2 Effects of plant genetic diversity on species richness, abundance and activity of herbivores, predators and parasitoids. Error bars represent 95% CI. Numbers next to error bars indicate number of studies in each category. Numbers in parentheses are Rosenberg's fail-safe numbers which indicate how many additional studies with effect size of 0 and of the same weight as the average of those already being used would need to exist to reduce the significance of the mean effect to 0.05. Effects are considered significantly different from 0 if 95% CI do not cross 0 (dashed line)

df = 3, *p* = .412). Similarly, both abundance and species richness of predators were significantly higher in genetically diverse plant stands (Figure 2; Q_m = 1.767, *df* = 1, *p* = .184). Plant genetic diversity had a marginally significant positive effect on species richness (Figure 2) and Shannon–Weiner diversity (*d* = 0.257, 95% CI −0.027 to 0.540, *N* = 2) of parasitoids while parasitoid abundance and parasitism rate were not significantly affected (Figure 2; Q_m = 4.322, *df* = 3, *p* = .228). For herbivores, only species richness was significantly increased with plant genetic diversity whereas herbivore abundance, damage and Shannon–Weiner diversity (*d* = 0.691, 95% CI −0.075 to 1.458, *N* = 2) were not affected (Figure 2, Q_m = 8.363, *df* = 3, *p* = .039). We found no significant relationship between responses of herbivores and their natural enemies (predators and parasitoids) to plant genetic diversity in studies which have assessed responses of both trophic groups in the same experiment (*r* = .028, *N* = 27, *p* = .891).

When herbivore feeding specialization was taken into account, it was found that damage by generalist herbivores was reduced in genetically diverse stands whereas damage by specialist herbivores was not significantly affected by plant genetic diversity (Figure 3; Q_m = 2.607, *df* = 1, *p* = .106). Abundance of neither generalist nor specialist herbivores was affected by plant genetic diversity (Figure 3; Q_m = 0.009, *df* = 1, *p* = .923).

Out of 60 studies included in the analysis, 38 were conducted on wild plant species and 22 on crops. We found some differences in arthropod responses to plant genetic diversity between natural and agricultural systems. Predator abundance was increased by plant genetic diversity in wild species (*d* = 0.444, 95% CI 0.126–0.762, *N* = 8), but not in crops (*d* = −0.003, 95% CI −0.452 to 0.445, *N* = 6; Q_m = 2.067, *df* = 1, *p* = .150). Similarly, herbivore abundance increased in genetic mixtures of wild species, but was reduced in mixtures of crop varieties (Figure 3; Q_m = 8.89, *df* = 1, *p* = .003). However, no difference in the effects of plant genetic diversity on herbivore damage was found between studies conducted on crops and wild plant species (Figure 3; Q_m = 0.366, *df* = 1, *p* = .545). Comparisons between crops and wild species could not be performed for other response variables (e.g. species richness) and other groups of arthropods due to a low number of studies in individual categories.

In studies on crops, monocultures were often represented by just a single crop variety of interest, such as a susceptible variety, with the aim to explore whether mixing this variety with others will help to reduce pest problems. We found no differences between crop genetic diversity effects on herbivore abundance when studies of a single plant genotype were compared to studies which replicated monocultures with different crop varieties (single variety: d = −0.277, 95% CI −0.585 to 0.030, N = 22; mixed varieties: d = −0.363, 95% CI −0.787 to 0.060, N = 17; Q_m = 0.196, df = 1, p = .658).

Both plant genetic and species diversity have been manipulated in 16 out of 60 reviewed studies, providing 110 effect sizes for comparison of plant genetic and species diversity effects on arthropods. The magnitude of the effect of plant genetic diversity on arthropods in studies which examined both effects of plant genetic and species diversity was not significantly different from that of plant species diversity effects (genetic diversity: d = 0.168, 95% CI 0.050–0.287, N = 55; species diversity: d = 0.170, 95% CI 0.019–0.320, N = 55; Q_m = 0.014, df = 1, p = .907). Similarly, no significant differences in effects of species and genetic diversity were revealed when comparisons were made separately for individual trophic groups of arthropods (Figure 4, p > .443). For predators and omnivores, only effects of plant genetic diversity were significantly different from zero (Figure 4).

4 | DISCUSSION

While previous meta-analyses have demonstrated significant effects of plant genetic diversity on community and ecosystem processes (Bailey et al., 2009; Whitlock, 2014), our meta-analysis is the first to explore the effects of plant genetic diversity on different trophic levels of arthropods, to integrate the results from ecological and agricultural experiments manipulating plant genotypic richness, and to compare the magnitudes of plant genetic and species diversity effects on arthropods. The overall magnitude of the effect of plant genetic diversity on arthropods in our analysis (d = 0.192) is almost identical to the magnitude of the effects of community-level responses to plant genotypic richness reported in a recent meta-analysis by Whitlock (2014) (d = 0.189) and, although significantly different from 0, can be considered as a small effect under Cohen's (1988) classification benchmarks. However, we found considerably larger positive effects of plant genetic diversity on species richness of arthropods, herbivores and predators (d = 0.540–0.626). Below, we discuss the mechanisms underlying the above effects, outline their implications for ecosystem functioning, arthropod conservation and pest management, and highlight the remaining knowledge gaps and future research directions.

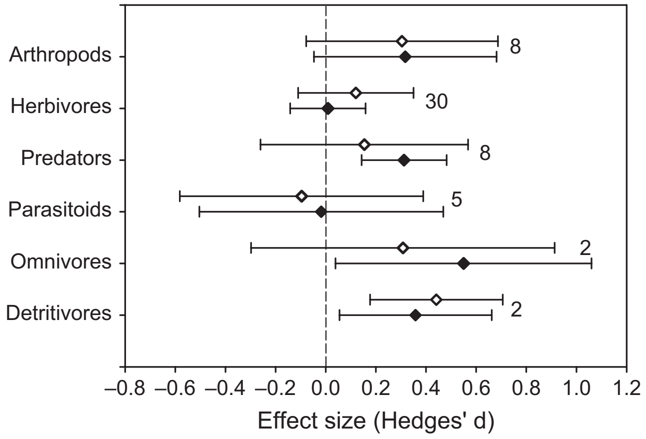

FIGURE 4 Comparison of the effects of plant genetic diversity (solid symbols) and species diversity (open symbols) on different trophic groups of arthropods. Only studies within which both plant species and genetic diversity have been manipulated were included in the analysis. Error bars represent 95% confidence intervals. Numbers next to error bars indicate number of studies for each trophic group. Effects are considered significantly different from 0 if 95% CI do not cross 0 (dashed line)

4.1 | Mechanisms of plant genetic diversity effects on arthropods

Positive effects of plant genetic diversity on arthropods can be due to additive and non-additive mechanisms (Hughes et al., 2008; Johnson et al., 2006). Additive effects result from independent influence of plant genotypes on arthropod communities such that arthropod responses in mixed stands can be predicted from arthropod responses in genetic monocultures. In contrast, non-additive effects cannot be predicted from measuring responses in monocultures and are due to interactions among genotypes in the mixture. For instance, plants often affect the phenotype of conspecific neighbouring plants (indirect genetic effects, Bailey et al., 2014) which results in changes in various plant traits and primary productivity that might, in turn, affect arthropods.

For cumulative responses such as arthropod species richness, the expected additive effect is an increasing function of the number of genotypes in a population, i.e. adding more genotypes will automatically result in higher species richness of the associated community if the communities differ between individual host genotypes (Hughes et al., 2008). However, the increase in arthropod species richness with plant genetic diversity observed in our meta-analysis is likely to be due to both additive and non-additive effects as both effects have been found in studies which have explicitly tested for the underlying mechanisms (Crawford & Rudgers, 2013; Crutsinger et al., 2006; Genung et al., 2010; Johnson et al., 2006; Tack & Roslin, 2011).

Effects of plant genetic diversity on arthropod abundance tended to be weaker than effects on arthropod species richness. The expected additive effect for ecological responses such as arthropod abundance which are expressed as means rather than a cumulative sum, is no change with the number of plant genotypes and any observed deviation from this expectation represents a non-additive effect (Hughes et al., 2008). Therefore, the fact that we found significant positive effects of plant genetic diversity on abundance of total arthropods and predators indicates the presence of non-additive effects of plant genetic diversity on abundance of these groups.

4.2 | Effects of plant genetic diversity on herbivores

Herbivores were the most studied trophic group of arthropods in the experiments manipulating plant genotypic richness. Several mechanisms can explain the observed increase in herbivore species richness in genetically diverse plant stands. Firstly, the number of herbivore species in plant communities composed of multiple genotypes can be higher due to the higher diversity of resources available to them (the resource specialization hypothesis, Hutchinson, 1959). Secondly, if plant primary productivity increases with genetic diversity then more herbivore individuals, and therefore more species, will be supported in genetically diverse plant stands (the more individuals hypothesis, Srivastava & Lawton, 1998). While a meta-analysis by Whitlock (2014) demonstrated that plant genotypic richness has a positive effect on plant productivity, supporting the assumption of the more individuals hypothesis, we did not find an overall increase in herbivore abundance in genetically diverse stands, suggesting that an increase in herbivore abundance is unlikely to be the main driver of increased herbivore species richness in genetically diverse plant stands. Instead, increased species richness of herbivores in genetically diverse mixtures is more likely to be explained by an increased diversity of resources, as predicted by the resource specialization hypothesis. Indeed, several studies which have examined the specific mechanisms behind the effects of plant genetic diversity on arthropods have found that increased diversity and amount of resources (e.g. number of flowers) in genetically diverse stands contributed to the observed herbivore response (Crutsinger et al., 2006; Genung et al., 2010; McArt, Cook-Patton, & Thaler, 2012).

Herbivore abundance decreased with an increase in crop genetic diversity, but increased with plant genetic diversity in wild plant species. Several factors might explain these differences in herbivore numerical responses to genetic diversity of cultivated and wild plants. Agricultural studies were usually focused on control of a single pest species by mixing crop genotypes with known differences in resistance to this pest, thus increasing the chances of associational resistance in genotypic mixtures (Root, 1973). In contrast, genotypes of wild plant species were usually selected at random and their relative susceptibility to herbivores was determined only afterwards as part of the experiment, potentially resulting in less dramatic differences in susceptibility to herbivores than between crop varieties. Moreover, in ecological field experiments plants were typically exposed to a wide variety of herbivores and it was therefore unlikely that any given plant genotype would be susceptible or resistant to all individual herbivore species (e.g. Barton et al., 2015), hence reducing the probability of associational resistance.

Another difference between studies on crops and wild plant species is that in many agricultural studies monocultures were represented by just a single crop variety of interest whereas in experiments on wild plants several plant genotypes were tested in monocultures. However, we found no differences between crop genetic diversity effects on herbivore abundance when studies of a single plant genotype were compared to studies which replicated monocultures with different crop varieties. This indicates that differences in herbivore responses to plant genetic diversity in agricultural and natural systems are not due to sampling effects and differences in experimental design used in agricultural and ecological studies. It is also unlikely that reduced abundance of herbivores in crop genetic mixtures in agricultural studies was due to increased top-down control by natural enemies as predator densities were not affected by crop genetic diversity.

The resource concentration hypothesis (Root, 1973) predicts that diverse plant communities should have lower abundance of specialist herbivores because of lower concentrations of their host plants in diverse stands as compared to monocultures. While this hypothesis was formulated to predict effects of plant species diversity on herbivores, it has been suggested that it can be extended to plant genetic diversity effects because specialist herbivores are known to distinguish between plant genotypes (Tooker & Frank, 2012). Contrary to the predictions of the resource concentration hypothesis, we found no effects of plant genetic diversity on the abundance of either specialist or generalist herbivores and significant negative effects of plant genetic diversity on damage by generalist herbivores but not by specialist herbivores, suggesting that genotype mixtures provide associational resistance against generalists but not specialists. This is in contrast to the results of meta-analyses on tree species diversity effects on herbivores which have shown that specialist herbivores are more negatively affected by increases in tree species diversity than generalists (Castagneyrol et al., 2014; Jactel & Brockerhoff, 2007; Kambach et al., 2016). This discrepancy may be due to different mechanisms of plant genetic and species diversity effects on herbivores. Unlike mixed-species plant stands, genetic mixtures of the same plant species have the same concentration of host plants as genetically poor stands. As a result, the overall density of specialist herbivores may not differ between genetically poor and rich stands and they may simply move from one genotype to another within the stand (Peacock & Herrick, 2000; Power, 1991; Utsumi, Ando, Craig, & Ohgushi, 2011). While in the case of specialist herbivores, this increased movement does not appear to lead to reduced herbivory, for generalist herbivores sequential feeding on different genotypes may reduce the rate of resource utilization and resulting plant damage (McArt & Thaler, 2013). However, our results for damage by generalist herbivores need to be considered with caution as they are based on only four studies and the fail-safe number is very small.

4.3 | Effects of plant genetic diversity on higher trophic levels

Previous studies exploring the relationship between plant species diversity and arthropod diversity have mostly shown that plant diversity effects dampen with increasing trophic level and are stronger for herbivores than for their natural enemies (Castagneyrol & Jactel, 2012; Scherber et al., 2010), but see Haddad et al. (2009). In contrast, we demonstrated stronger effects of plant genetic diversity on predators and parasitoids than on herbivores, suggesting that plant genetic diversity effects can cascade (and amplify) up the food web. These results disagree with the notion that plant genetic variation should have weaker effects on higher trophic levels because few plant traits are specific to attracting or deterring natural enemies (Johnson & Agrawal, 2005) and suggest an intriguing possibility that plant genetic diversity causes shifts in trophic structure of associated arthropod communities (Haddad et al., 2009). Such shifts might have important implications for ecosystem functioning and ecosystem services as trophic groups of arthropods have been shown to differ in their functional importance, with herbivores being the most functionally important (Scherber et al., 2010). Moreover, the finding that more genetically diverse plant communities support more species-rich communities of arthropods is important because high species richness at multiple trophic levels has stronger positive effects on ecosystem services than richness in any individual trophic group (Soliveres et al., 2016). Therefore, loss of plant genetic diversity is likely to result in a loss of arthropod species diversity across several trophic levels which might amplify negative impacts of plant genetic impoverishment on ecosystem functioning.

Effects of plant genetic diversity on higher trophic levels can be direct (Grettenberger & Tooker, 2017; Ninkovic, Al Abassi, Ahmed, Glinwood, & Pettersson, 2011), mediated by increase in herbivore abundance and species richness (Abdala-Roberts et al., 2016; Moreira & Mooney, 2013), or driven by trait-mediated indirect effects (Johnson et al., 2006; Jones et al., 2011). The fact that we found stronger effects of plant genetic diversity on predators and parasitoids than on herbivores (Figure 1) and no significant relationship between responses of herbivores and their natural enemies suggests that mechanisms independent of herbivore abundance may be more important. Moreover, increases in predator species richness in genetically diverse stands can also be driven by higher predator abundance (in accordance with the more individuals hypothesis).

Natural enemies can also mediate effects of plant genetic diversity on herbivores through top–down effects. The enemies hypothesis (Root, 1973; Russell, 1989) predicts that more diverse plant communities will increase abundance and diversity of natural enemies of insect herbivores by offering a higher diversity of alternative food resources and refuges, which will result in a better control of herbivore densities by natural enemies in more diverse plant stands. The results of our meta-analysis provide partial support for the enemies hypothesis because we found positive effects of plant genetic diversity on predators and parasitoids. However, we did not find a significant effect of plant genetic diversity on parasitism rates and overall herbivore abundance and damage and there was no significant relationship between responses of herbivores and their natural enemies to plant genetic diversity. While predation has not been directly measured in the experiments included in our meta-analysis, it is possible that the observed reduced damage by generalist herbivores in genetically diverse stands could be due to increased predation. In contrast, specialized natural enemies such as parasitoids and specialized herbivores appear to be less affected by plant intraspecific diversity.

4.4 | Comparison of plant genetic and species diversity effects on arthropods

Because trait variation within a single species is usually lower than among multiple species, one might expect intraspecific diversity effects to be smaller than species diversity effects (Cook-Patton et al., 2011). Contrary to this prediction, we found similar effects of plant genetic diversity on arthropods in studies where both plant genetic and species diversity have been manipulated. This result agrees with a recent meta-analysis by Des Roches et al. (2018) which demonstrated that the magnitude of ecological effects of variation within a species was comparable to the effects of replacement or removal of that species (species effects). However, the magnitude of the plant genetic and species diversity effects in our meta-analysis was smaller than in several recent meta-analyses using the same measure of effect size (Hedges' *d*) and assessing the effects of plant species diversity on arthropods. For instance, Letourneau et al. (2011) reported much larger effects of crop species diversification on herbivores ($d = -1.34$) and natural enemies ($d = 2.20$) whereas Jactel and Brockerhoff (2007) reported a moderate negative effect ($d = -0.67$) of tree species diversity on herbivory in forests. Smaller effect sizes in our meta-analysis could be due to the fact that we compared effects of plant genetic and species diversity on arthropods only when these effects were assessed within the same study using the same or parallel experimental setup. This removed many potential confounding variables such as the use of different plant and arthropod species in different studies and differences in methodology. In addition, in most of the studies comparing plant genetic and species diversity effects on arthropods included in our analysis, arthropod responses were measured on a single focal plant species. For instance, in species diversity experiments, arthropod diversity or abundance on a single plant species in monocultures of that species was compared to arthropod diversity or abundance on the same plant species in species mixtures. Therefore, our results cannot be used as an indicator of magnitude of community-level responses of arthropods to plant species diversity at plot level.

While the overall magnitude of the effects of plant genetic and species diversity on arthropods was similar, our analyses revealed several important differences in the patterns of plant genetic and species diversity effects on arthropods. For instance, we have shown that, in contrast to plant species diversity effects, plant genetic diversity effects increased with the arthropod trophic level and were stronger for generalist herbivores than for specialist herbivores. These results hint at differences in the underlying mechanisms of plant genetic and species diversity effects on arthropods and suggest that the hypotheses and mechanisms underlying plant species diversity effects on arthropods cannot be always extrapolated to effects of plant genetic diversity. Overall, our results highlight the importance of incorporating both inter- and intraspecific diversity into predictions of the effects of biodiversity loss.

4.5 | Implications for arthropod conservation and pest management

Significant positive effects of plant genetic diversity on species richness of different trophic groups of arthropods indicate that genetic impoverishment within plant populations may have community-level consequences, and emphasizes the importance of maintaining high levels of plant genetic diversity for arthropod conservation (Bangert et al., 2005). The approach to use plant genetic diversity for arthropod conservation depends on whether the mechanisms of plant genetic diversity on arthropod species richness are additive or non-additive (Johnson et al., 2006). If the effects are additive, it might be worth focusing conservation efforts on those particular genotypes that come with diverse associated communities. However, if the effects of plant genetic diversity are non-additive, then both the number and type of plant genotypes to conserve need to be considered. While we were not been able to distinguish between additive and non-additive mechanisms in our meta-analysis, individual studies which have differentiated between the above mechanisms have found both additive (Johnson et al., 2006; Tack & Roslin, 2011) and non-additive effects (Crawford & Rudgers, 2013; Crutsinger et al., 2006; Genung et al., 2010) of plant genetic diversity on arthropod diversity, suggesting that both the number and the type of plant genotypes need to be considered for arthropod conservation.

The results of our meta-analysis provide limited support for the suggestion that genotypically diverse cultivar mixtures can be used as an effective pest management tool (Tooker & Frank, 2012). While herbivore abundance was lower in genetically diverse crops, there was no significant decrease in overall herbivore damage and no increase in abundance of predators. This is in marked contrast to the strong negative effects of crop species diversity on herbivores and strong positive effects of intercropping on natural enemies of herbivores revealed in a meta-analysis by Letourneau et al. (2011). Therefore, it is unlikely that mixtures of crop cultivars or varieties will provide as successful control of agricultural pests as increases in interspecific diversity of crops.

However, we found that crop genetic mixtures reduced damage by generalist herbivores (although this result was based only on four studies). Therefore, more studies are needed to explore the possible use of crop genotypic mixtures against generalist pests, particularly because intercropping is not very effective against generalist herbivores with increasing plant species diversity in a stand often leading to increased damage by generalist herbivores (associational susceptibility, Letourneau, 1995). Moreover, mixtures of crop cultivars can have positive effects even if they do not reduce herbivore abundance and damage. For instance, Power (1991) showed that while abundance of English grain aphids was not affected by oat genetic diversity, aphid movement rates were significantly higher and plant tenure times significantly lower in the genetically diverse oat populations, which significantly reduced the incidence of the aphid-transmitted barley yellow dwarf virus. In addition, crop genetic mixtures have been very successful in reducing the spread of fungal pathogens, particularly in cereal crops (Mundt, 2002; Zhu et al., 2000). Unlike plant resistance to herbivores, plant resistance to pathogens is controlled by individual genes, and pathogens spread within plant stands passively. Increase in frequency of pathogen-resistant genotypes in a stand creates a physical barrier against the spread of the infection, whereas insect pests can circumvent this barrier by actively moving between plants within stands (Wilhoit, 1992). Therefore, crop genetic diversity appears to be more effective for controlling diseases than pests. Finally, a recent meta-analysis by Reiss and Drinkwater (2017) revealed that cultivar mixtures have higher crop yield than monocultures, and the above diversity effects are stronger under disease pressure and abiotic stressors. Cultivar mixtures thus promote increased diversity, yield and yield stability in agroecosystems.

4.6 | Limitations, knowledge gaps and future research directions

Our review is based on studies which have manipulated plant genetic diversity experimentally by creating genetic monocultures and mixtures of several genotypes. Tack, Johnson, and Roslin (2012) argued that estimates of plant genetic diversity effects in such studies might be inflated because diversity experiments are usually performed in small common gardens whereas the genotypes for the experiments are often collected from a wide area. However, a meta-analysis by Whitlock (2014) demonstrated that the effects of genotypic richness were not significantly affected by the mismatch in sampling scale between the plant genotype collection sites and the sizes of experimental plots used. Moreover, any disparity in sample scale is not very relevant for the interpretation of results of studies conducted in agricultural systems as in agriculture different crop species and varieties are often planted together regardless of their geographic origin. However, another drawback of studying ecological effects of plant genetic diversity by manipulating the number of plant genotypes is that this approach treats genotypes as discrete categories and ignores variation in the extent of genetic and phenotypic differences in ecologically important traits among and within plant genotypes in a population. Therefore, we advocate that future studies should manipulate the amount of genetic variance in phenotypic traits, as opposed to just the number of genotypes.

While we compared the magnitude of plant species and genetic diversity effects on arthropods when these effects were explored within the same study, we were not able to explore potential interactions between plant species and genetic diversity effects because only a handful of studies had incorporated such interactive effects within the experimental design by manipulating plant genetic diversity at different levels of plant species diversity and vice versa (Campos-Navarrete, Munguia-Rosas, Abdala-Roberts, Quinto, & Parra-Tabla, 2015; Crawford & Rudgers, 2013; Hahn et al., 2017). These results from the above studies suggest that the species richness of plant communities can modify the effects of plant genetic diversity on arthropods. Understanding the interactions between plant genetic and species diversity effects is important for predicting the impact of biodiversity loss on communities and ecosystems because changes in plant species and genetic diversity might be causally linked (Vellend & Geber, 2005) and losses of genetic diversity in plant populations may affect the rate of species diversity decline (Booth & Grime, 2003). Therefore, future studies should explore the potential interactions between plant species and genetic diversity effects on arthropods.

The majority of examined studies have focused on the effects of plant genetic diversity on herbivores and their natural enemies. Other groups of arthropods such as omnivores and detritivores were severely underrepresented. For instance, we are only aware of a single study exploring plant genetic diversity effects on pollinators (Genung et al., 2010) and two studies examining the effects of plant genetic diversity on ground-dwelling arthropods and arthropods associated with plant litter (Crutsinger, Reynolds, Classen, & Sanders, 2008; Kanaga et al., 2009). To the best of our knowledge, no studies have examined the effects of plant genetic diversity on below-ground arthropods. As a result, we do not currently have a good understanding of the consequences of losses of plant genetic diversity for pollination ecosystem services, below-ground herbivory and nutrient cycling performed by the soil and litter arthropods. Future studies of plant genetic diversity effects should focus on these understudied groups of arthropods.

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AUTHORS' CONTRIBUTIONS

J.K. conceived the idea for this study, J.K. and D.H. collected the data, J.K. performed the analyses and led the writing of the manuscript.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Repository https://doi.org/doi:10.5061/dryad.mp1bk57 (Koricheva & Hayes, 2018).

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SUPPORTING INFORMATION

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