Weed Science

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Review

Neutral weed communities: the intersection between crop productivity, biodiversity, and weed ecosystem services

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Cite this article: Esposito M, Westbrook AS, Maggio A, Cirillo V, DiTommaso A (2023) Neutral weed communities: the intersection between crop productivity, biodiversity, and weed ecosystem services. Weed Sci. **71**: 301–311. doi: 10.1017/wsc.2023.27

Received: 13 March 2023
Accepted: 2 May 2023
First published online: 11 May 2023

Associate Editor:
William Vencill, University of Georgia

Keywords:
Artificial intelligence; crop–weed coexistence; functional diversity; niche overlap; non-detrimental weed communities; sensor technology; species-specific weed identification; sustainable weed management

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Abstract

Weeds are a fundamental component of agroecosystems and, if not appropriately managed, can cause severe crop yield losses. New perspectives on weed management are required, because current approaches, such as herbicide application or soil tillage, have significant environmental and agronomic drawbacks. We propose the concept of "neutral weed communities," which are weed communities that coexist with crops and do not negatively affect crop yield and quality compared with weed-free conditions. Management practices that promote neutral weed communities can enable reduced use of herbicides and soil tillage while enhancing ecosystem services and biodiversity. We report scientific evidence of neutral weed communities and survey ecological explanations for why different weed communities have different effects on crop production. We also propose two weed management approaches for attaining neutral weed communities. The first approach aims to maximize weed biodiversity using traditional approaches such as cropping system diversification and integrated weed management. Higher weed biodiversity is associated with lower dominance of competitive weed species that reduce crop yield. The second approach relies on modern tools such as robots and biotechnology to manipulate the density of specific weed species. This approach can remove highly problematic species and minimize niche overlap between the weeds and crops. Given the complexity of interactions among crops, weeds, and other components of the agroecosystem, we highlight the need for multidisciplinary research to illuminate mechanisms that determine the neutrality of weed communities.

Introduction

Weeds are a fundamental component of agricultural systems and may interact with crops and other organisms in several ways. Weeds can negatively impact crop production by competing with crops. When weeds are not appropriately managed, they can reduce yields of major crops by a global average of 34% (Oerke 2006). World food demand is rising, driven by population growth and other factors (van Dijk et al. 2021). Thus, farming activities such as managing agricultural weeds play an increasingly key role in assuring food security. Given the nearly 5 billion ha of cropland and pastures worldwide (FAOSTAT 2020), it is equally important to minimize the negative environmental impacts of agricultural production. Unfortunately, current weed control strategies may be largely unsustainable. Intensive tillage and herbicide use are associated with environmental risks and herbicide resistance. Environmental risks associated with intensive tillage include soil erosion (Seitz et al. 2018), decreases in soil quality (Karlen et al. 2013), soil organic matter losses (Haddaway et al. 2017), nutrient depletion (Gadermaier et al. 2012), and soil compaction (Orzech et al. 2021). Longer-term, tillage-based systems can lead to a high carbon footprint (Dachraoui and Sombrero 2020) and yield reductions (Kok et al. 2009). Currently, 267 weed species (154 dicots and 113 monocots) have shown resistance to herbicides (Heap 2023), and this number is growing.

Even if optimal long-term weed control could be achieved without negative externalities, it might not be desirable to remove all weeds from agricultural fields (Maxwell 2018). From a conservation perspective, weeds are an important component of agroecosystem biodiversity. The oversimplification of agricultural systems, associated with intensive herbicide use, has reduced the abundance and diversity of weed species (Storkey and Westbury 2007 and references therein). In addition to reducing plant diversity, removing too many weeds from agricultural fields can contribute to declines in species at higher trophic levels (Bretagnolle and Gaba 2015; Marshall et al. 2003; Smith et al. 2020). Fields with low biodiversity also tend to be dominated by a few highly competitive weed species that may be very difficult to control (Storkey and Neve 2018).

Against this background, it is necessary to identify new weed management strategies to reduce herbicide application and soil tillage while maintaining crop yield, ecosystem service provisioning, and biodiversity. These strategies should reflect knowledge about the ecological interactions between weeds and crops, which vary depending on morpho-functional traits of the weeds and crops. In this paper, we introduce the concept of "neutral weed communities." These are communities that coexist with the crops and do not significantly reduce crop yield or quality compared with weed-free conditions. Although the term "neutral weed communities" is new, there already exists substantial evidence that not all weed communities are deleterious to crop production (Adeux et al. 2019; Brooker et al. 2020; Gibson et al. 2017; Rowntree et al. 2021).

If a weed community does not cause major crop yield or quality losses, weed management actions can be reduced and some weeds conserved for ecosystem service provisioning and maintenance of biodiversity (MacLaren et al. 2019). Promoting neutral weed communities is therefore an effective method of enhancing the sustainability and long-term productivity of agricultural systems. We propose two approaches to attaining neutral weed communities. The first approach focuses on increasing weed biodiversity, whereas the second relies on selecting specific weed species for conservation or elimination. Both strategies will help shift weed community composition from undesirable to desirable weed species, which is a major aim of ecological weed management (Liebman et al. 2001).

The goals of this review are:

1. to describe advantages associated with the promotion of neutral weed communities ("Benefits of Promoting Neutral Weed Communities");
2. to provide an overview of neutral weed communities in different agricultural contexts ("Evidence of Neutral Weed Communities");
3. to survey ecological explanations for why some weed communities are neutral with respect to crops ("Understanding the Ecology and Biology of Neutral Weed Communities"); and
4. to identify current and emerging weed management strategies to attain neutral weed communities ("How to Attain Neutral Weed Communities")

Benefits of Promoting Neutral Weed Communities

Promoting neutral weed communities would enable farmers to reduce the frequency and intensity of weed control operations. Consequently, the economic costs and environmental drawbacks associated with weed control operations would also be reduced. In addition, weeds may have positive effects on crops or the surrounding environment. For example, weeds provide resources for beneficial arthropods (Bàrberi et al. 2010; Marshall et al. 2003; Null et al. 2003) and birds (Gibbons et al. 2006; Vickery et al. 2002). By providing these resources, weeds contribute to regulating ecosystem services such as crop pollination (Garibaldi et al. 2014; Nicholls and Altieri 2013). In addition, weed species can reduce soil erosion (Seitz et al. 2018) and improve soil physical properties (Arai et al. 2014). Some weeds improve soil nutrient content, such as nitrogen (Promsakha Na Sakonnakhon et al. 2006), phosphorus (Ojeniyi et al. 2012), potassium (Ojeniyi et al. 2012), and carbon content (de Rouw et al. 2015). Mechanisms by which weeds might increase crop yield are further discussed in the section "Facilitative Weed–Crop Interactions."

In addition to influencing yield, weeds often affect crop quality. It is possible that some weed mixtures could improve crop profitability by increasing crop quality (Gibson et al. 2017). In a 2-yr field experiment, Millar et al. (2007) studied the impact of three levels of interspecific competition on seed development and quality of soybean [*Glycine max* (L.) Merr.]. The seed protein content was highest under the most intense weed competition in both years, while seed yield was not affected by interspecific competition in the first year. However, greater weed competition reduced seed yield in the second year, which was much drier than the first year. Water scarcity might have made weed interference more intense, considering the water-stress resistance of dominant weed species, including cocklebur (*Xanthium strumarium* L.), ivyleaf morningglory (*Ipomoea hederacea* Jacq.), fall panicum (*Panicum dichotomiflorum* Michx), and common ragweed (*Ambrosia artemisiifolia* L.).

Some authors have suggested capitalizing on the stress resistance and plasticity of weeds to realize more sustainable and diversified cropping systems. In India, Gholamhoseini et al. (2013) grew corn (*Zea mays* L.) in monoculture or mixture with an agricultural weed, redroot pigweed (*Amaranthus retroflexus* L.), at different nitrogen and water levels over 2 yr. They reported that the mixture used water and nitrogen inputs more efficiently and achieved higher forage yield and quality relative to the corn monoculture. This work aligns with other studies that consider the potential of arable weeds as intercrops or living mulches (Germeier 2000; Rowntree et al. 2021). Although the remainder of our review focuses on shaping resident weed communities rather than planting additional non-crop species, both lines of inquiry are valuable.

Evidence of Neutral Weed Communities

Not All Weed Communities Reduce Crop Yield

Weed communities can both cause severe crop yield losses (Oerke 2006) and provide benefits to crops and the broader environment (Blaix et al. 2018; Gaba et al. 2020; Kleiman et al. 2021; Smith et al. 2020). A growing body of research suggests that the competitive effects of weeds on crops depends on a multitude of factors, including the functional composition of weed communities, crop traits, and environmental conditions (Bàrberi et al. 2018; Cirillo et al. 2018; Gaba et al. 2017; Gunton et al. 2011). Under some circumstances, weed communities may provide ecosystem services without affecting crop yield and quality. In this review, we define such weed communities as neutral weed communities. In France, Adeux et al. (2019) identified six weed communities over 3 yr of observations that included weed biomass, weed density, and winter cereal crop biomass. Two of the six communities identified did not significantly reduce grain yield compared with weed-free treatments. These two communities did not consistently have lower weed density or biomass than the communities that did reduce grain yield. The two neutral weed communities were mostly composed of Persian speedwell (*Veronica persica* Poir.), common chickweed [*Stellaria media* (L.) Vill], cutleaf geranium (*Geranium dissectum* L.), ivyleaf speedwell (*Veronica hederifolia* L.), and catchweed bedstraw (*Galium aparine* L.).

In Italy, Esposito et al. (in press) obtained similar results, identifying neutral weed communities in a field experiment with winter wheat (*Triticum aestivum* L.) under three different soil

https://doi.org/10.1017/wsc.2023.27 Published online by Cambridge University Press

nutrient levels (low, optimal, and surplus). Under surplus nutrition, one detrimental community was identified. This finding suggests that high soil fertility may promote the growth of dominant weed species that capitalize on high rates of fertilization to compete aggressively with crops (Little et al. 2021). Under both low and optimal nutrient levels, one neutral weed community and one detrimental community were identified. The neutral communities did not negatively affect grain yield or quality. Corn chamomile (*Anthemis arvensis* L.) was the most abundant weed in neutral communities, accounting for 28% and 46% of total weed density in optimal and low nutrient treatments, respectively. The relative density of this species was higher in neutral communities than in detrimental communities. Under optimal nutrition, *S. media* was present only in the neutral community, while *V. persica* was mostly present in the neutral weed community. The annual legume California burclover (*Medicago polymorpha* L.) apparently contributed to the detrimental communities by accumulating a large amount of aboveground biomass and causing wheat lodging. *Medicago polymorpha*, which is native to the Mediterranean region and adapted to semiarid conditions (Yousfi et al. 2015), may also compete with crops for water. Under optimal and low nutrition, *M. polymorpha* was mostly present in the detrimental communities compared with the neutral communities. Finally, Esposito et al. (in press) noted that the density of the neutral community was higher than the density of the detrimental weed community under optimal nutrition, suggesting that density is not always a good predictor of a weed community's deleterious effect on crop yield.

Boström et al. (2003) studied the relationship between weed community composition and yield losses in spring wheat and barley (*Hordeum vulgare* L.; syn.: *Hordeum distichum* L.) in 33 field trials over 3 yr. Weeds such as scarlet pimpernel (*Anagallis arvensis* L.), nightflowering catchfly (*Silene noctiflora* L.), *Euphorbia* spp., field violet (*Viola arvensis* Murray), common lambsquarters (*Chenopodium album* L.), and *Polygonum* spp. were not associated with yield losses. In contrast, wild radish (*Raphanus raphanistrum* L.) and hempnettle (*Galeopsis* spp.) were among the most detrimental species, causing large crop yield losses.

In a 26-yr experiment in Sweden, Milberg and Hallgren (2004) ranked weed species from the most benign to the most detrimental. Using 1,691 samples from on-farm trials, they identified benign weeds as those consistently occurring in situations with small cereal yield losses and detrimental weeds as those associated with larger yield losses. In autumn-sown cereals, benign weed species included wild buckwheat [*Polygonum convolvulus* L. var. *convolvulus*; syn.: *Fallopia convolvulus* (L.) Á. Löve], prostrate knotweed (*Polygonum aviculare* L.), false cleavers (*Galium spurium* L.), field forget-me-not [*Myosotis arvensis* (L.) Hill], *S. media*, and *Veronica* spp. Benign weed species in spring-sown cereals were *P. convolvulus*, *Lamium* spp., and wallflower mustard (*Erysimum cheiranthoides* L.). Detrimental weed species were scentless mayweed [*Tripleurospermum inodorum* (L.) Sch. Bip.] and shepherd's purse [*Capsella bursa-pastoris* (L.) Medik.] in autumn-sown cereals and *Galeopsis* spp. and curlytop knotweed [*Polygonum lapathifolium* L.; syn. *Persicaria lapathifolium* (L.) Gray] in spring-sown cereal systems.

Similarly, in winter wheat, Jones and Smith (2007) grouped weeds as very desirable, desirable, and undesirable based on agronomic issues and biodiversity benefits. Out of the 18 very desirable or desirable weeds identified in this study, 6 species were also defined as benign by Milberg and Hallgren (2004). Analogously, *S. media* was classified as very desirable by Jones and Smith (2007). This species was representative of neutral weed communities in winter wheat according to Esposito et al. (in press). These points of agreement between different studies suggest that certain weed species are relatively benign in several cereal-cropping systems, although any species can be harmful given the right conditions.

Much research on the relative competitiveness of different weed species and communities has been carried out in Europe. However, evidence from other world regions also exists. In an arid region of India, Bhandari and Sen (1979) showed that sowing an annual leguminous weed, *Indigofera cordifolia* B. Heyne ex Roth, improved growth parameters and yield in millet [*Pennisetum glaucum* (L.) R. Br.] and sesame (*Sesamum indicum* L.). Millet yield was 19.8% higher and sesame yield was 22.4% higher in plots sown with *I. cordifolia*, compared with weeded plots. In the same area, weeds like Arabian-primrose [*Arnebia hispidissima* (Lehm.) A. DC.], *Spermacoce articularis* L.f., and feather cockscomb (*Celosia argentea* L.) increased the growth parameters and yield of millet but not sesame (Sen [1978] as cited by Bhandari and Sen [1979]).

This survey reveals that much research on weed community competitiveness has focused on annual cropping systems. One reason is that annual crops account for much more harvested cropland area than perennial crops (FAOSTAT 2020). However, evidence for neutral weed communities has also emerged from perennial cropping systems. Liang and Huang (1994) highlighted the need to distinguish beneficial from detrimental weeds in citrus orchards. They noted that some weeds do not compete substantially with the citrus trees, instead providing economic and ecological benefits. Beneficial weeds, such as tropical ageratum (*Ageratum conyzoides* L.), sessile joyweed [*Alternanthera sessilis* (L.) R. Br. ex DC.], and many dicotyledonous weeds, often had soft tissues, shallow roots, and broad leaves. In contrast, detrimental weeds, such as goosegrass [*Eleusine indica* (L.) Gaertn.], cogongrass [*Imperata cylindrica* (L.) P. Beauv.], bermudagrass [*Cynodon dactylon* (L.) Pers.], large crabgrass [*Digitaria sanguinalis* (L.) Scop.], and many monocotyledonous weeds, had opposite characteristics. Liang and Huang (1994) considered *A. conyzoides* one of the most beneficial weeds, because it can support natural enemies of citrus pests and is suitable as a green manure. Other weeds reported to be beneficial in citrus orchards include *C. argentea*, alligatorweed [*Alternanthera philoxeroides* (Mart.) Griseb.], Chinese giant-hyssop [*Agastache rugosa* (Fisch. & C.A. Mey.) Kuntze], beefsteakplant [*Perilla frutescens* (L.) Britton], and *Exallage auricularia* (L.) Bremek. (Liang and Huang 1994 and references therein).

Neutral weed communities have also been identified in other orchard types. In a 3-yr experiment in organic and conventional apple (*Malus domestica* Borkh.) orchards in China, Meng et al. (2016) demonstrated the possibility of managing pernicious weeds in the organic orchard by propagating Indian mock strawberry [*Duchesnea indica* (Andrews) Teschem.; syn. *Potentilla indica* (Andrews) Th. Wolf]. This native species was able to suppress undesirable weeds through competition, enabling good weed suppression without the use of herbicides. Despite the fast growth of *P. indica* and its increasing dominance in the understory ground cover of the organic orchard, apple yield was not different between the organic and conventional orchards in the last 2 yr of the study. In a comparison between organic and conventional olive (*Olea europaea* L.) groves in Greece, organic and conventional groves did not differ in edible olive yield or olive oil yield (Solomou and Sfougaris 2011). Wild carrot (*Daucus carota* L.) and ovate goatgrass (*Aegilops geniculata* Roth) were the most frequently occurring herbaceous plants in 10-yr and 6-yr certified organic groves, respectively.

Caveats

Data on which weeds are most detrimental or beneficial can be used to focus weed management efforts on maximizing crop productivity and ecosystem services, rather than removing all weeds. Such data should be collected in diverse climates and cropping systems, as the identities of "detrimental" and "beneficial" weed species will vary from place to place. Several species characterized as benign by the studies discussed in this section are highly problematic in other contexts. Notably, different crops may display different degrees of competitiveness against weeds (Andrew et al. 2015; Corre-Hellou et al. 2011; Lemerle et al. 2014). Consequently, neutral weed communities are more likely to occur in more competitive crops, such as wheat, barley, and corn. In addition, it is important to note that the effect of a particular weed species depends not only on climate and cropping system but also on the presence of other weed species. Species-level data cannot always substitute for community-level analysis.

Researchers and stakeholders should also adopt a multiyear perspective when considering neutral weed communities and how they should be managed. It is not advisable to modify weed management without considering how this decision will change plant community composition over time. Even if a weed community is unlikely to cause yield loss in the current year, eliminating weed control operations might allow high levels of weed seed production, increasing the soil seedbank and potentially contributing to yield loss in future years. This consideration becomes especially important when a farmer makes weed control decisions in a competitive crop, but then grows a less competitive crop in a later phase of the rotation cycle. We advocate holistic analysis of the long-term costs and benefits of weeds and management tactics.

Understanding the Ecology and Biology of Neutral Weed Communities

Coexistence between Weeds and Crops

To understand why weed communities are not always detrimental, it is useful to draw on broader theories of plant–plant coexistence. A foundational idea in ecology is the concept of competitive exclusion, that is, the idea that two or more species that occupy the same niche cannot coexist (Gause 1934). According to this paradigm, stable coexistence of multiple species is best explained by differences in their functional traits (i.e., differences in how they respond to and affect their biotic and abiotic environments). For example, species might require different resources at different times. Even among plants, all of which require similar resources, there is substantial potential for resource partitioning to promote coexistence (Silvertown 2004). Resource partitioning is one of several proposed stabilizing mechanisms of coexistence, defined as mechanisms that increase the magnitude of negative intraspecific interactions relative to negative interspecific interactions (Chesson 2000). In general, intraspecific interactions do tend to be more negative than interspecific interactions in plant communities, consistent with stabilizing mechanisms of coexistence (Adler et al. 2018). In the presence of stabilizing mechanisms of coexistence, equalizing mechanisms (i.e., mechanisms that reduce fitness differences between species) may further promote stable coexistence (Chesson 2000). Alternatively, equalizing mechanisms could help support models of unstable coexistence. Notably, Hubbell (2001) proposed a neutral theory in which drift, migration, and speciation are more important than stabilizing mechanisms and fitness differences. Niche-based and neutral theories are not mutually exclusive: stabilizing mechanisms and fitness differences between species do exist, but their magnitudes and effects on community assembly can vary (Adler et al. 2007). The uncovering of mechanisms promoting coexistence is ongoing and crucial research, especially given that such mechanisms may maintain ecosystem function as well as biodiversity (Godoy et al. 2020; Turnbull et al. 2013).

In applying ecological perspectives to agricultural situations, one should remember that (1) most cropping systems are frequently disturbed and therefore best characterized as early successional habitats, and (2) the effects of weeds on crops are more frequently measured than the effects of crops on weeds. For both reasons, a report of weeds that do not appear to impact crop yield does not constitute a report of stable coexistence. Nevertheless, arguments developed to explain coexistence in natural systems can provide helpful insights into agroecological dynamics. For instance, niche complementarity (a lack of niche overlap, often reflecting different spatiotemporal resource use patterns) is a primary explanation for higher yields in some intercropping systems relative to monocultures of the component species (Brooker et al. 2015). This overyielding in polyculture indicates that interspecific interference is less detrimental than intraspecific interference, implying that stabilizing mechanisms such as resource partitioning are at work. Other mechanisms, including facilitation, may also contribute to the success of intercropping systems (Brooker et al. 2015).

In the context of agricultural weeds, greater niche overlap between weed species and crop species may increase weed–crop competition (Zimdahl 2004). Weeds that consume the same resources as the crop during the same time periods are typically more problematic than weeds with different requirements. More broadly, functional similarity between weeds and crops may involve shared morphological, physiological, or phenological traits (Navas 2012). Shared traits sometimes reflect homology (common descent); therefore, understanding weed phylogeny could contribute to a better understanding of weed–crop competition (Gibson et al. 2017). The effects of functional traits on ecological interactions between weeds and crops can be observed in the absence of weed control. However, it is also true that similarities between weeds and crops complicate efforts to develop selective weed control tactics and that weed management programs often inadvertently favor weeds that are similar to crops. This unintentional selection promotes crop mimicry in weeds. For example, early water grass [*Echinochloa oryzoides* (Ard.) Fritsch] closely resembles rice (*Oryza sativa* L.) (Barrett 1983).

One of the principal drivers of weed–crop competition and weed community assembly is the diversity of available resource pools. According to the resource pool diversity hypothesis, an increase in the spatiotemporal diversity of soil resource pools leads to decreased crop yield loss per unit of weed density (Smith et al. 2010). This trend occurs because diverse soil resource pools enable more resource partitioning among species. The negative relationship between resource pool diversity and crop yield loss is particularly strong when weeds and crops have different resource acquisition traits (i.e., greater capacity for niche differentiation). At the same time, resource pool diversity shapes weed community structure and may support the persistence of species that are functionally different from the crop. Overall, the resource pool diversity hypothesis predicts that practices such as crop rotation, cover cropping, use of diverse fertility amendments, and integrated weed management will reduce the dependence of crop yield on weed abundance (Smith et al. 2010). More generally, the relationship between weed abundance and yield loss is affected by environmental factors, management factors, and weed community composition (Ryan et al. 2010; Swinton et al. 1994; Wilson and Wright 1990).

Agricultural activities represent filters that shape the species and functional composition of weed communities (Armengot et al. 2016; Cordeau et al. 2021; Mhlanga et al. 2015). Higher-strength values of these filters (intensive agriculture) are associated with reduced weed diversity and increased abundance of a few dominant weed species (Adeux et al. 2019; Storkey and Neve 2018). Conversely, a greater diversity of weak filters can select for more diverse and less damaging weed communities. Examples of practices to promote these more-neutral weed communities include integrated weed management, crop management diversity in space and time, and organic fertilizer application (MacLaren et al. 2020).

Recent research suggests that increased weed diversity (i.e., coexistence among many species) is associated with reduced crop yield loss. Understanding the role of weed functional diversity in maintaining ecosystem function and preventing yield loss is among the top five research priorities in weed science, according to a group of experts (Neve et al. 2018). The next subsection summarizes existing knowledge about the relationship between diversity and yield.

Increased Weed Diversity Is Associated with Reduced Crop Yield Loss

Negative relationships between weed species richness and crop yield loss have been demonstrated by several authors. Storkey and Neve (2018) identified such a relationship using data from the long-term Broadbalk winter wheat experiment, which was initiated in 1843. In this experiment, weedy and weed-free plots were maintained under different fertilization regimes. Using weed species richness data from 19 yr of the experiment, the authors found a strong negative correlation between weed species richness and percentage yield loss due to weeds. This finding was used to illustrate the hypothesis that increased weed diversity is associated with reduced crop yield loss when the weed diversity reflects habitat heterogeneity. Weed species diversity in heterogenous habitats generally implies functional diversity and the presence of species that do not compete strongly against crops. This hypothesis by Storkey and Neve (2018) expands on the resource pool diversity hypothesis (Smith et al. 2010) described in the previous subsection. Separately, Storkey and Neve (2018) also hypothesized that weed seedbank diversity is a useful indicator of agronomic and environmental sustainability. In a different study, Brooker et al. (2020) reported a positive relationship between total weed species richness and barley biomass.

Crop yield loss may also be negatively associated with weed evenness or diversity indices combining richness with evenness. Yield was positively correlated with evenness and the Shannon and Simpson indices in coconut (*Cocos nucifera* L.) and banana (*Musa × paradisiaca* L.) (Cierjacks et al. 2016). In a long-term study (1996 to 2011), greater weed diversity was associated with a greater capacity for soybean yield increase (Ferrero et al. 2017). However, greater weed diversity also interacted with cold temperatures to reduce corn yield; this result could not be fully explained (Ferrero et al. 2017). Adeux et al. (2019) reported that more diverse weed communities generally produced less weed biomass and caused lower crop yield losses. Over the gradient of weed community evenness, weed biomass decreased by 83% and crop productivity increased by 23%. It was not possible to separate the effect of reduced weed biomass from any direct effect of weed diversity on crops. However, this study did support the hypothesis that higher weed diversity is associated with lower dominance of competitive weed species that are likely to cause substantial yield loss.

Future research is needed to understand why greater weed diversity is associated with reduced dominance of highly competitive weed species. As noted earlier, this association does not necessarily reflect a causal relationship. However, it is also true that processes of weed–weed interference become more significant in diverse weed communities, sometimes limiting the growth of competitive weed species (Adeux et al. 2019; Clements et al. 1994; Pollnac et al. 2009). Real-world weed communities are multispecies assemblages in which complex interspecific interactions occur with variation in space and time. Continued study of these interactions may provide insight into the negative association between weed community diversity and weed–crop competition (Adeux et al. 2019).

Thus far, this section has focused on the competitive effects of weeds on crops. It is worth reiterating that these effects, and therefore the prevalence and composition of neutral weed communities, should be expected to vary between cropping systems and environments. In the following subsection, we turn to the topic of positive weed–crop interactions, which are similarly context specific.

Facilitative Weed–Crop Interactions

Facilitation occurs when the presence of one organism improves the survival, growth, or reproduction of another organism. Facilitative interactions among plants have been well recognized in plant ecology (Brooker et al. 2008; Callaway 2007; Hunter and Aarssen 1988). In agriculture, facilitative interactions have frequently been reported between crops grown in mixture (Brooker et al. 2021; Li et al. 2007; Ren et al. 2014). Facilitative interactions among crops may involve numerous mechanisms, including the production of root exudates to enhance biological nitrogen fixation (Li et al. 2016) or mobilize nutrients (Li et al. 2014) and hydraulic lift (Sekiya and Yano 2004; Sekiya et al. 2011). Given that these facilitative interactions can occur between different crop species, it is reasonable to assume that they might also occur between weeds and crops. Facilitative interactions between weeds and crops may also be indirect and mediated by beneficial insects or soil microbes.

Facilitative effects of weeds mediated by beneficial insects involve ecosystem services such as pollination or biological control of crop pests. The potential of weeds to promote crop pollination is an active area of research, as demonstrated by recent studies in oilseed rape (*Brassica napus* L.; Crochard et al. 2022), mango (*Mangifera indica* L.; Kleiman et al. 2021), and sweet cherry [*Prunus avium* (L.) L.; Gilpin et al. 2022]. This topic merits further study. In contrast, the potential of weeds to promote biological control has been established for decades (Altieri and Whitcomb 1979). For example, a study in corn showed that pests such as fall armyworm (*Spodoptera frugiperda* Smith & Abbot), corn leaf

https://doi.org/10.1017/wsc.2023.27 Published online by Cambridge University Press

aphid (*Rhopalosiphum maidis* Fitch), and sap beetles (*Colopterus* spp.) were less abundant in weedy plots compared with weeded plots (Penagos et al. 2003). Predators of corn pests, such as the carabid *Calosoma calidum* Fabricius, were more abundant in weedy plots. Corn yield did not differ significantly between weedy and weed-free plots, suggesting that conservation of some weeds may be a reasonable method of enhancing biological control (Penagos et al. 2003). In that study, the most abundant weed species were purple nutsedge (*Cyperus rotundus* L.), niruri (*Phyllanthus niruri* L.), *E. indica*, and garden spurge (*Euphorbia hirta* L.). Similarly, Brust (1991) found that the activity of beneficial nematodes was higher in weedy corn plots relative to weed-free plots, whereas Patriquin et al. (1988) found that black bean aphids (*Aphis fabae* Scopoli) were less numerous in weedy faba bean (*Vicia faba* L.) plots relative to weed-free plots. Moreover, no significant corn and faba bean yield reduction was reported in weedy plots compared with weed-free plots (Brust et al. 1991; Patriquin et al. 1988). DiTommaso et al. (2016) reported that common milkweed (*Asclepias syriaca* L.) harbored aphids, which provided food for parasitoid wasps (*Trichogramma* spp.) and other beneficial insects that attack the eggs of insect pests such as the European corn borer (*Ostrinia nubilalis* Hübner). This positive effect of *A. syriaca* offset its negative (competitive) effect on corn. Consequently, the role of *A. syriaca* in promoting biological control increased the economic injury level of this weed (i.e., the minimum weed density at which weed control is worth the cost).

Soil microorganisms can play a crucial role in modulating positive plant–plant interactions (Rodríguez-Echeverría et al. 2013). Weeds can be a source of beneficial soil microorganisms such as bacteria that promote crop growth (Sarathambal et al. 2014; Sorty et al. 2016; Sturz et al. 2001). In addition, some agricultural weeds are strong hosts of arbuscular mycorrhizal fungi (AMF), although many weeds are weak AMF hosts (Vatovec et al. 2005). A meta-analysis showed that weak host weeds tend to show negative responses to AMF (Li et al. 2016). Even strong host weeds tend to exhibit lower plant growth responses to AMF than strong host crops under fertilized conditions (Li et al. 2016). These findings support the view that AMF can contribute to both crop yield and weed suppression. Additional research has suggested that the presence and appropriate management of AMF host weeds may be harnessed to promote AMF colonization of annual crops (Brito et al. 2013; Feldmann and Boyle 1999). The potential for plant facilitation through mycorrhizal symbiosis might be increased when the plants involved are phylogenetically distant (Montesinos-Navarro et al. 2019) and differ in their AMF assemblages (Montesinos-Navarro et al. 2012). Therefore, a diverse weed community may be more likely to enhance AMF colonization of a crop, relative to a weed community dominated by a few aggressive species that are weak AMF hosts.

Other forms of plant facilitation may involve plant responses to signals emitted by neighbors, such as volatile organic compounds (VOCs). Signals including VOCs may trigger biochemical responses that positively or negatively affect plant performance, depending on the plant species and signal (Baluška and Mancuso 2009; Brosset and Blande 2022; Gagliano and Renton 2013; Vivaldo et al. 2017). A better understanding of signaling between weeds and crops could provide further insight into why different weed communities have different effects on crop production.

This section has explored ecological mechanisms that may help explain the presence of neutral weed communities in agroecosystems. In the following section, we consider how this ecological knowledge can be applied to promote the establishment of neutral weed communities.

How to Attain Neutral Weed Communities

Here, we propose two approaches to attain neutral weed communities (Figure 1). These approaches are intended to promote sustainable weed management, enable reduced herbicide use and soil tillage, and increase biodiversity without significant crop yield losses. The first approach focuses on maximizing weed diversity, whereas the second approach focuses on selectively removing the most problematic weed species.

As described previously, weed species diversity is frequently associated with functional diversity and reduced crop yield loss. The main mechanism underlying reduced crop yield loss is a reduction in the dominance of highly competitive weed species that consume the resources crops require. Weed diversity can be enhanced through management practices that increase environmental heterogeneity and the potential for niche complementarity between weeds and crops (Navas 2012; Smith et al. 2010; Storkey and Neve 2018). Practices aimed at increasing crop diversity, such as crop mixtures, crop rotation, and cover cropping, are valuable tools to increase weed biodiversity and reduce yield loss (Palmer and Maurer 1997; Smith et al. 2010). Other strategies include diversifying residue management programs and fertility sources to support weeds with different resource use profiles (Smith et al. 2010). In the context of weed management, integrated programs combining diverse tactics result in higher weed diversity and better long-term outcomes, compared with less diverse programs that are heavily reliant on one or two tactics (Clements et al. 1994; Cordeau et al. 2020; Liebman 2018; Liebman and Gallandt 1997). The capacity of a management system to simultaneously promote weed biodiversity and crop yield may vary with crop identity, environmental conditions, and the weed species present in an area (Mézière et al. 2015). Further research is needed to develop systems that promote diverse and neutral weed communities in each context. In addition, research is needed to develop strategies for managing aggressive weed species that impede efforts to increase weed community diversity (Armengot et al. 2017). These species may require specific control measures, that is, the application of our second approach.

Species-specific weed management (Figure 1) can be accomplished in several ways. Humans are often capable of identifying and removing troublesome weed species by hand. However, hand weeding is laborious and expensive (Tiwari et al. 2022). Emerging technologies provide more efficient methods of removing specific weed species, such as competitive species that show substantial niche overlap with the crop. We suggest that these technologies can be used to establish weed communities “shaped” according to the ecology of each cropping system, drastically reducing weed–crop interference.

Some approaches to species-specific weed management involve sensor-equipped field robots or drones (Zhang et al. 2022; Figure 2). The sensors measure features such as weed shape, size, color, texture, and spectral reflectance, then artificial intelligence can be used to identify weed species based on these features (Bawden et al. 2017; Pantazi et al. 2016; Peteinatos et al. 2020; Wang et al. 2022). Accurate weed identification represents a major challenge, as individuals of the same weed species can frequently appear different. Other issues include the difficulty of identifying young seedlings and variable light availability (Zhang et al. 2022). Despite these challenges, classification accuracy is improving with

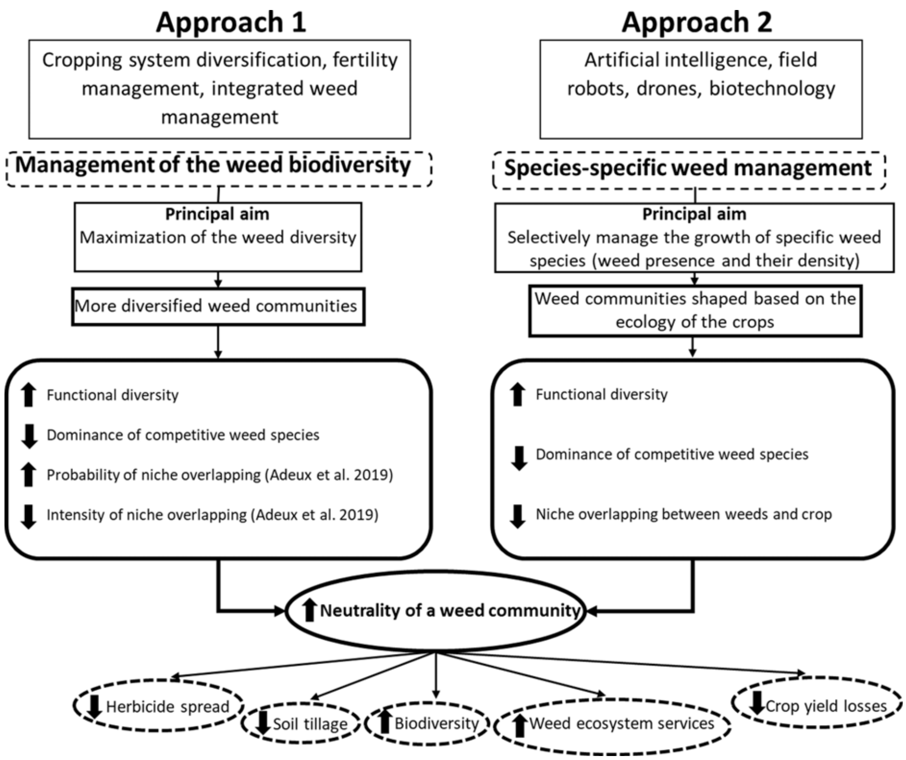

Figure 1. Schematic representation of the principal aims and ecological effects of two approaches proposed to increase the neutrality of weed communities. The first approach can be pursued by applying traditional management strategies (Adeux et al. 2019). The second approach may be facilitated by emerging technologies.

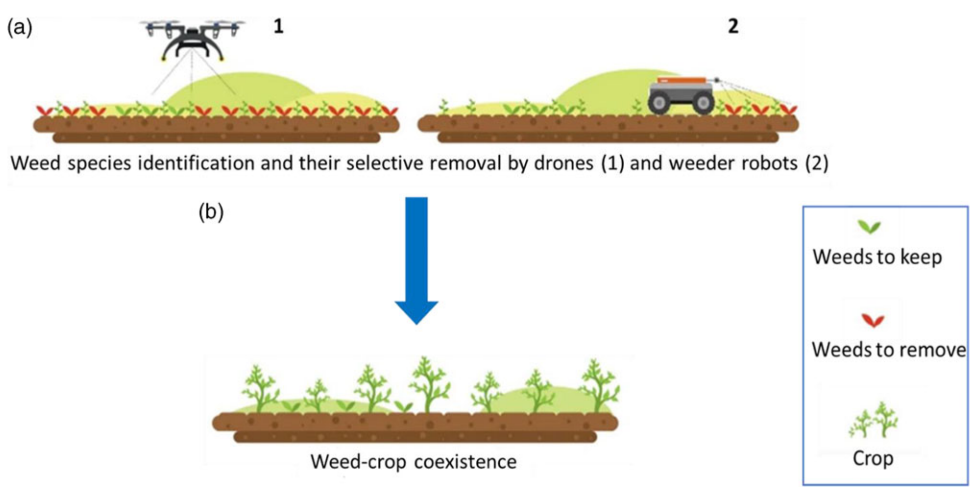

Figure 2. Using drones and weeder robots to promote neutral weed communities. (A) Weed community manipulation with (1) drones and (2) weeder robots capable of recognizing and removing specific weed species. (B) Crop coexistence with a neutral weed community. Modified from Esposito et al. (2021).

the emergence of new machine learning and deep learning strategies, combined with the creation of large training image sets (Zhang et al. 2022). For example, Olsen et al. (2019) used numerous labeled images of eight Australian weed species and deep learning to achieve a greater than 95% classification accuracy. Du et al. (2022) used approximately 10,000 images of flax (*Linum usitatissimum* L.) and associated weeds to develop convolutional neural network models, one of which achieved 90% classification accuracy when deployed in a flax field.

Once identified, weeds that require control can be mechanically or chemically removed. Detection and removal of the targeted weed species may both be performed by a single terrestrial unit (Zhang et al. 2022). Alternatively, some authors have suggested combining aerial drones with terrestrial robots. In this scenario, unmanned aerial vehicles fly over a crop field and take aerial images, which are analyzed by an off-site system that sends information about the locations of problematic weeds to terrestrial robots that perform weed removal (Esposito et al. 2021; Figure 2). Buddha et al. (2019) developed an image-analysis procedure that identified three corn weed species with 93.8% accuracy from RGB images taken from a high altitude (24.4 m). The weed locations and identifications would be sent to a robotic sprayer. Similarly, in sugar beet (*Beta vulgaris* L.), Lottes et al. (2017) identified two weed species with 85% precision from aerial images. Such promising

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results should encourage further research, which will increase the ability of robotic tools to selectively remove specific weed species without causing collateral damage (i.e., damage to beneficial weeds or crops).

New biotechnologies also show promise for selective weed management. In particular, RNA interference (RNAi) enables the silencing of specific gene targets. Agricultural research on RNAi is largely focused on controlling insect pests (Kunte et al. 2020; Mamta and Rajam 2017). However, RNAi might also allow the control of troublesome weed species without affecting desirable plants or other organisms (Mezzetti et al. 2020). To achieve this selectivity, small interfering RNA molecules would need to silence gene sequences that are important in the target species but not present in desirable species. Further research is needed to develop this technology and determine what level of selectivity is possible.

Conclusion

In this paper, we have provided scientific evidence of neutral weed communities in different cropping systems. We have also explored ecological mechanisms that help explain why different weed communities have different effects on crops. We emphasize that a weed community that is neutral in one cropping system and environment may be detrimental in other contexts. More studies are needed to understand the interactions between neutral weed communities and crops and to identify neutral weed communities in diverse cropping systems and environments. Further research is needed on neutral weed communities in the context of crop rotation, as a weed community that is neutral in one rotation phase could be detrimental in the next phase. Whenever possible, research on these questions should occur over long timeframes and assess indirect and positive interactions between weeds and crops as well as direct negative interactions such as competition.

We proposed two weed management approaches to attain neutral weed communities. The first approach seeks to maximize weed biodiversity and can be pursued with existing ecological weed management practices. The second approach seeks to selectively manage specific weed species. Advanced tools such as weeding robots may increase the feasibility of this second approach. Using these approaches to promote neutral communities could contribute to decreased weed control costs, enhanced ecosystem services, and increased biodiversity without reducing crop productivity.

Acknowledgments. We thank current and former members of the DiTommaso Cornell Weed Ecology and Management Laboratory and Maggio Laboratory at the University of Naples Federico II for engaging discussions and feedback on this work. We thank David Clements and Richard Smith for providing valuable suggestions for improving the article. This research received no specific grant from any funding agency or the commercial or not-for-profit sectors. No competing interests have been declared.

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