Phytochemistry / Fitoquímica

The role of phytochemical diversity in the management of agroecosystems
El papel de la diversidad fitoquímica en el manejo de los agroecosistemas

Francisco Javier Espinosa-García

Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán, Mexico.
Author for correspondence: espinosa@cieco.unam.mx

Abstract

Biodiversity in ecosystems is crucial in providing ecosystem services and their stability and resilience. However, most studies supporting the benefits of biodiversity in crop health were studied at the cultivar scale, generally without specifying the resistance mechanisms involved in the resistance of crops to pests. Thus, it is unclear if phytochemical diversity is one of those resistance mechanisms and whether the ecosystem patterns and processes in which phytochemical diversity is involved can be replicated or adapted to the management of sustainable agroecosystems. Here, I review the roles of phytochemical diversity in natural ecosystems and determine if they can be helpful in the management of agroecosystems. I briefly review (a) the spatial and temporal structure of phytochemical diversity in ecosystems and its effect on plant consumers; (b) how that diversity is generated and maintained; and (c) the current or potential role of phytochemical diversity in agroecosystems. The α-, β-, and γ-phytochemical diversities are very high in ecosystems and landscapes; phytochemical diversity gets displayed in dynamic mosaics of mixtures of secondary metabolites that vary in their concentration and composition within and among individuals, populations, or species. Phytochemical diversity is fostered by evolutionary or coevolutionary processes, mainly under an arms-race scenario. The patterns and processes of phytochemical diversity are idiosyncratic depending on the identity of the interacting species and the local biotic and abiotic environment; thus, to copy them to industrial agroecosystems is hardly viable. However, five recommendations in which phytochemical diversity could be helpful in agroecosystem management are made.

Keywords: α-phytochemical diversity, β-phytochemical diversity, γ-phytochemical diversity, arms-race coevolution, industrial agroecosystems, plant secondary metabolites, traditional agroecosystems.

Resumen

La biodiversidad en los ecosistemas es crucial para su estabilidad y resiliencia. Sin embargo, la mayoría de los estudios que apoyan los beneficios de la biodiversidad en la fitosanidad se han hecho a escala de cultivar, generalmente sin especificar los mecanismos implicados en la resistencia de los cultivos a las plagas. Así, no está claro si la diversidad fitoquímica (DF) es uno de esos mecanismos de resistencia y si los patrones y procesos ecosistémicos en los que interviene pueden ser adaptados al manejo de agroecosistemas sustentables. Se examinaron las funciones de la DF para determinar su utilidad potencial enfocándose en (a) la estructura espacial y temporal de la DF y su efecto sobre los consumidores de plantas; (b) cómo se mantiene la DF y (c) el papel actual o potencial de la DF en los agroecosistemas. Se encontró que las DF α, β y γ son muy elevadas en los ecosistemas; la DF se despliega en mosaicos dinámicos de mezclas de metabolitos secundarios que varían en su concentración y composición dentro y entre individuos, poblaciones o especies. La DF es fomentada por procesos ecológicos y evolutivos entre las plantas y sus agonistas y antagonistas. Se concluye que los patrones y procesos de la DF son idiosincrásicos dependiendo de las especies que interactúan en un entorno particular. Así, copiarlos a los agroecosistemas industriales no es viable, pero se hacen cinco recomendaciones en las que la DF podría ser útil en el manejo de agroecosistemas.

Palabras clave: agroecosistemas industriales, agroecosistemas tradicionales, coevolución de carrera armamentista, diversidad fitoquímica α, diversidad fitoquímica β, diversidad fitoquímica γ, metabolitos secundarios de las plantas.

S pecies biodiversity in ecosystems is crucial in providing ecosystem services and their stability and resilience (Oliver *et al.* 2015a, b). It has been proposed that increased biodiversity prevents the devastation of species by herbivores and pathogens in an ecosystem (Pautasso *et al.* 2005, Jactel & Brockerhoff 2007). However, epidemics, or recurrent generalized insect attacks in cycles of several years may occur on a few species of trees in natural ecosystems (Hicke *et al.* 2006, Robert *et al.* 2020). Devastating attacks may also fall upon a species that can lead to its local extinction when the pathogen is an introduced invasive species, as in the case of Dutch elm disease (Gibbs 1978, Davidson *et al.* 1999).

The replication of natural ecosystem processes and patterns in agroecosystems is a strategy to improve the stability and resilience of cultivated systems, particularly in crop health (Altieri *et al.* 1995, Gliessman *et al.* 1998). However, replicating structures and processes from natural ecosystems to agricultural systems has been questioned since natural ecosystems' structure, nutrient and energy flow, and regeneration differ fundamentally from agroecosystems (Denison & McGuire 2015).

Increased biodiversity of species and genotypes in agroecosystems has been implemented after epidemics, or disastrous pests have wiped out genetically homogeneous monocultures (Tooker & Frank 2012). Crop rotation, polycultures, and weed tolerance within and outside of crop plots are also practiced to increase biodiversity to control pests and pathogens in agroecosystems (Risch *et al.* 1983, Landis *et al.* 2000, Kremen & Miles 2012). Some of those agricultural practices have been inspired by natural ecosystems (Gliessman *et al.* 1998, Gliessman 2011). Other biodiversity-enhancing practices have been inspired by traditional agricultures or empirical developments of farmers (Wezel *et al.* 2014, González Jácome 2021). Despite the criticisms and the source of inspiration used to implement practices in cultivated systems, there is agreement that agroecosystems that are more biodiverse in space and time provide more ecosystem services than agroecosystems with low biodiversity (Letourneau *et al.* 2011, Kremen & Miles 2012, Oliver *et al.* 2015b). However, most studies on the benefits of biodiversity in the interactions between plants and the species that consume them have been conducted at the species scale and the level of varieties, cultivars, or genetic variation of a crop, almost always without specifying the resistance mechanisms involved in those interactions (Ode 2006, Letourneau *et al.* 2011, Tooker & Frank 2012). Thus, it is unclear if phytochemical diversity is one of those resistance mechanisms and if the patterns and processes in which it is involved can be replicated or adapted for the management of sustainable agroecosystems. This paper aims to review the role of phytochemical diversity in ecosystems under the premise that part of the structure and processes in which phytochemical diversity is involved in natural ecosystems can be adapted to agroecosystems. First, I briefly review the spatial and temporal structure of phytochemical diversity in ecosystems and its effect on plant consumers. Then, I summarize how the phytochemical diversity structure is generated and maintained by interactions between plants and other species. Finally, I briefly examine the current or potential role of phytochemical diversity in agroecosystem management, considering that there is a high diversity of agroecosystems along a gradient from industrial or conventional agriculture to traditional agriculture (González Jácome 2003, 2021) and that crops have undergone domestication processes that affect their phytochemical diversity.

Phytochemical diversity in ecosystems: structure and function

Phytochemical diversity can be analyzed at different spatio-temporal scales (García-Rodríguez *et al.* 2012, Wetzel & Whitehead 2020) ([Table 1](#)). At the scale of structural diversity, the nearly 200,000 secondary metabolites described so far represent a variety of molecular arrangements ranging from isoprene (68.2 g mol^{-1} to polymers such as natural rubber latex ($600,000$ g mol^{-1}). Many secondary metabolites affect more than one metabolic target (Hu & Bajorath 2013, Singh *et al.* 2021), so that one molecule can affect several species, and the effect depends on the concentration of the molecule to which a plant antagonist or agonist species is exposed (Gershenzon & Dudareva 2007, Hadacek *et al.* 2011, García-Rodríguez *et al.* 2012, Moore *et al.* 2014). Thus, the functional diversity of secondary metabolites exceeds their structural diversity and is critical in the interactions between plants and their agonists and antagonists, as they are involved in plant defense and signaling between plants and other organisms.

Table 1. Classification of the phytochemical diversity. Translated and modified from García-Rodríguez *et al.* (2012).

Type of diversity	Spatial scale	Time context
Alpha phytochemical diversity PDα	That which occurs in mixtures of secondary metabolites (SM) present in plant tissues. Its description includes the number of SM structures (richness) together with the abundance of each of them in a plant tissue. This results in the profile or chemical phenotype of the tissue. The set of tissue chemical phenotypes constitutes the chemical phenotype of the individual.	(a) The ontogeny of an individual or plant tissue; (b) a moment in time; (c) in different seasons; (d) the same tissue before and after the attack of a biotic or abiotic stress agent.
Beta phytochemical diversity at the individual scale PDβi	The degree of turnover in SM composition among the chemical phenotypes of the different tissues of a plant.	(a) Among the tissues or organs within an individual plant; (b) differences in the same tissue over time or along environmental gradients; (c) comparing the same tissue before and after the effect of a biotic or abiotic stress agent.
Beta phytochemical diversity at the population scale PDβp	The degree of turnover in the composition of individual chemical phenotypes of a species: (a) within a population; or (b) between populations of a species.	(a) At a point in time; (b) across generations
Gamma phytochemical diversity PDγ	The richness of individual secondary metabolites or chemical phenotypes in the plant communities that make up a landscape. Degree of differentiation between individuals of different species that make up a community or landscape.	(a) Across seasons. (b) Across generations

Plant secondary metabolites (PSM) are found in complex mixtures within and among plant tissues and vary according to the ontogeny of individuals and their organs, the fitness value of those tissues or organs, and in response to biotic and abiotic environmental stress (Langenheim 1994, Courtois *et al.* 2012, Gershenzon *et al.* 2012). Moreover, all that variation is regulated by the genotype, and the PSM mixtures found in an individual at a given time differentially affect the species interacting with plants. Thus, an additional level of functional phytochemical diversity is attributable to PSM mixtures, which act on species interacting with plants, including natural enemies of herbivores and pathogens (Ode 2006, Züst *et al.* 2012, Bravo-Monzón *et al.* 2014).

There may be compounds within a mixture that by themselves intoxicate or repel a plant antagonist, although it is more likely that several compounds act against the attacker in an additive or synergistic manner (Espinosa-García & Langenheim 1991b; García-Rodríguez *et al.* 2021, Macel *et al.* 2005, Richards *et al.* 2016). The relative importance of the activity of single compounds and mixtures varies with the host range of plant attackers. Generalist attackers are more inhibited by medium or high concentrations of mixtures than specialists, which can override the toxicity

of mixtures and single compounds and exploit them in the localization of their plant host (Richards *et al*. 2016, García-Rodríguez *et al*. 2021). However, nullifying the toxicity of secondary metabolites is costly unless herbivores sequester them and use them in their defense; hence, high concentrations of mixtures will adversely affect specialist herbivores (Cipollini *et al*. 2014, Petschenka & Agrawal 2016).

At the population or plant community scale in the tropics, the diversity of secondary metabolite mixtures is associated with high herbivore diversity and low herbivory, although the predominance of specialists or generalists in the herbivore community varies with the plant taxonomic group examined (Richards *et al*. 2015, Salazar *et al*. 2018).

Structural and functional phytochemical variation in space and time is also combined with variation in nutrient content for plant-consuming species (Au *et al*. 2013, Wetzel *et al*. 2016). This combination forms "dynamic chemical mosaics" (Whitham 1983) of phenotypes in tissues, individuals, populations, communities, and landscapes that select consumer species that can take advantage of mosaics and exclude those that cannot take advantage of them. Thus, dynamic mosaics' variation can be considered a defensive trait (Nyman 2010, Wetzel & Thaler 2016, Pearse *et al*. 2018, Glassmire *et al*. 2019). The phytochemical mosaics prevalent in one population commonly differ from those of other populations (Züst *et al*. 2012, Bravo-Monzón *et al*. 2014), and those characterizing one species differ from those of other species in plant communities (García-Rodríguez *et al*. 2012, Coley *et al*. 2018, Salazar *et al*. 2018).

The level of plant resistance to pests and pathogens has been related to the heterogeneity of the dynamic mosaic composition of structural, functional, and nutritional phytochemical diversity (Wetzel *et al*. 2016, Glassmire *et al*. 2019). However, the homogeneity or heterogeneity in phytochemical diversity in terms of resistance will depend on the specific pest or pathogen (Espinosa-García *et al*. 2021). For example, heterogeneity for a generalist consumer, such as *Phytophthora cinnamomi*, which can attack about 5,000 plant species belonging to more than 40 families (Hardham & Blackman 2018), will be different from that of a specialist such as the Abert's squirrel, which discriminates the chemotypes of pine trees of the same species when feeding on them (Snyder 1992). The heterogeneity of phytochemical diversity also affects natural enemies of herbivores or pathogens, as the plant's chemical composition can positively or negatively affect natural enemies (Ode 2006, Pearse *et al*. 2018, Hauri *et al*. 2021). Thus, phytochemical diversity affects top-down and bottom-up herbivore population regulation acting directly on herbivores or their natural enemies (Peñaflor & Bento 2013, Bálint *et al*. 2016, Massad *et al*. 2017, Gasmi *et al*. 2019).

At the community scale, odors emitted by different species may hinder or facilitate the location of herbivore hosts or insect predators and parasitoids depending on the composition of the species neighborhood (Barbosa *et al*. 2009). Moreover, the complex network of volatile signals emitted by plants and their herbivores in seasonal forests results from an "arms race" type of coevolution. Plants make themselves difficult to locate, and herbivores refine their host detection ability by utilizing plant volatiles (Gershenzon *et al*. 2012, Zu *et al*. 2020).

The increase in phytochemical diversity has been assumed to be beneficial for plant defense: the higher the phytochemical diversity, the more effective the defense (Kubo & Hanke 1985, Jones *et al*. 1991, Richards *et al*. 2015, Espinosa-García *et al*. 2021, García-Rodríguez *et al*. 2021). The few tests of this hypothesis show that the increased diversity of the phytochemical makeup of populations and plant lineages is associated with less herbivory (Bravo-Monzón *et al*. 2014, Becerra 2015), but in a low-elevation plant community, the negative relationship between increased phytochemical diversity and herbivory holds, whereas at a high elevation community the relationship reverses (Fernandez-Conradi *et al*. 2021). Moreover, such a relationship was not found at a clonal crop scale (Espinosa-García *et al*. 2021). In experimental settings where phytochemical mixtures of varying diversity are assayed on herbivores or pathogens, mixtures perform better against generalist fungal pathogens but not always against specialists (García-Rodríguez *et al*. 2021); increased phytochemical richness in the mixtures did not affect herbivores and pathogens, but single compounds of some mixtures were active against one or more plant consumers. Then, the more phytochemical diversity, the more plant consumers were negatively affected, and the compounds' activities depended on the consumer identity (Whitehead *et al*. 2021). Therefore, a high phytochemical diversity at the individual, populational and community scales should protect plants against the local assemblage of herbivores. However, the degree of phytochemical diversity and its activity on plant consumers may vary depending on environmental gradients and the identity of the species that consume plants in a locality (Glassmire *et al*. 2019, Bakhtiari *et al*. 2021, Fernandez-

Conradi *et al*. 2021). Nevertheless, the random addition of plant secondary metabolites to a mixture does not assure its efficacy because antagonist interactions among the PSM may occur, and the plant consumers may detoxify that mixture (Whitehead *et al*. 2021). Likewise, the sole addition of new phytochemical variants in a population does not imply increased stability or resistance against the local assemblage of consumers for the same reasons that may operate at the mixture scale (Espinosa-García *et al*. 2021). Thus, the novel phytochemical combinations must undergo natural selection, leaving the combinations that add up to the plants' fitness or the population's persistence.

Generation and maintenance of phytochemical diversity structure in populations and communities

Phytochemical diversity is maintained and structured according to evolutionary processes (coevolution and adaptation) fostered by interactions between plants and the agonist or antagonist species that consume them (Becerra *et al*. 2009, Speed *et al*. 2015, Whitehead *et al*. 2021). The modes of natural selection (diversifying, frequency-dependent, and stabilizing) in those processes may promote, limit, or stabilize phytochemical polymorphisms in populations (Cates *et al*. 1983, Sturgeon & Mitton 1986, Snyder 1992, Moore *et al*. 2014, Bracewell *et al*. 2018, Kessler & Kalske 2018).

Those natural selection modes imply diffuse coevolutionary processes in which phytochemical diversity (α, β, and γ) is shaped by the species that depend on plants, and the community of plant enemies and mutualists is shaped by phytochemical diversity (Glassmire *et al*. 2016, 2020, Kessler & Kalske 2018). The shaping of phytochemical diversity by plant enemies can be different, and even opposite, depending on the specialization of the enemies (generalists vs. specialists), if they are keystone enemies or the identity of each one of them (Macel *et al*. 2005, Stam *et al*. 2014, Poelman & Kessler 2016, Massad *et al*. 2017, Glassmire *et al*. 2020, Cuny *et al*. 2021). Thus, phytochemical polymorphisms, with several or many variants are expected in plant populations, where individual plants in a population will have phenotypes varying in their resistance and vulnerability to different sets of plant enemies (Squillace *et al*. 1985, Langenheim 1994, Linhart *et al*. 2005, Iason *et al*. 2012).

A mechanism that promotes and maintains phytochemical diversity is diffuse coevolution (Bakhtiari *et al*. 2021, Volf *et al*. 2018), which contributes to the variation in chemical profile among populations of a plant species (Macel *et al*. 2004, Linhart *et al*. 2005, Bravo-Monzón *et al*. 2014, Martínez-Díaz *et al*. 2015) as the herbivore assemblages attacking that species vary among populations, causing local adaptation of plants to those assemblages (Züst *et al*. 2012, De-la-Cruz *et al*. 2020). Selection pressure from local consumers acts on phytochemical variation produced by gene drift, founder effects, or that correlated with plant adaptation to local abiotic factors (Linhart & Grant 1996, Defossez *et al*. 2021). That process is consistent with the geographical mosaic hypothesis of coevolution in which the coevolutionary outcome of the interaction of a plant species with a particular species of a plant consumer can be agonistic, antagonistic or neutral depending on the local set of herbivores, pathogens, and mutualists (Thompson 2001). The local non-focal plant consumers are affected by the changes in the chemical profile of the focal plant and local diffuse coevolutionary process can occur. Hence, those local coevolutionary processes would promote the phytochemical differentiation among populations of a plant species (Bravo-Monzón *et al*. 2014, 2018, Martínez-Díaz *et al*. 2015).

The processes producing differences in the phytochemical makeup among populations are relevant for crops that are disseminated by people away from their original place of domestication; the crops in new agroecosystems may have different sets of agonists and antagonists that may change the crops' phytochemistry. As domestication *in situ* is a continuous process (Casas *et al*. 2007), where peasants foster the adaptation of crops to the new local biotic and abiotic conditions producing new varieties (Johannessen *et al*. 1970), new phytochemical variants are expected.

A critical issue in the persistence of plant populations and communities is the degree of phytochemical differentiation among individuals or plant species, as perceived and processed by plant consumers (Becerra 2007, Sedio *et al*. 2017, Volf *et al*. 2018). In agroecosystems, polymorphisms of individual phenotypes are thought to be relevant for the persistence of crops preventing the evolution of resistant strains or biotypes of plant enemies capable of annihilating plant populations (Pimentel & Bellotti 1976, Gershenzon & Dudareva 2007, Gershenzon *et al*. 2012).

Phytochemical differentiation, or dissimilarity, is produced by the change in the chemical phenotypes in the expression of novel PSM or through new configurations of the ensemble of preexisting PSM in a population or community. The new arrangements may include changes in the relative concentrations of the PSM and the absence of compounds in a phenotype expressed by other individuals (*e.g.*, Becerra 1997). The phytochemical differentiation among of co-occurring woody plant species is much greater in a tropical rainforest than in temperate forests (Sedio *et al*. 2018) and in North American temperate forests, the differentiation among co-occurring species increases with precipitation and temperature (Sedio *et al*. 2021).

The phytochemical differentiation within (Robinson *et al*. 2022) and among individuals in a population, and its differential effects on plant consumers and their natural enemies, has been extensively documented with chemotypes, polymorphic chemical phenotypes, induced changes in the chemical phenotype after the attack of a plant antagonist, or the dynamic mosaics discussed previously (Espinosa-García & Langenheim 1991a, Wheeler 2006, Padovan *et al*. 2013, Bustos-Segura *et al*. 2015, Richards *et al*. 2015, Bálint *et al*. 2016, Meléndez-González & Espinosa-García 2018, Espinosa-García *et al*. 2021). Likewise, the differentiation among plant species in communities affecting directly or indirectly the structure of the second or third trophic levels is well documented (Becerra 2007, Richards *et al*. 2015, Glassmire *et al*. 2016, Salazar *et al*. 2018, Volf *et al*. 2018, Fernandez-Conradi *et al*. 2021). As dissimilarity increases among plant taxa, the host breadth gets reduced and specialists predominate in the herbivore community (Becerra 2007, Volf *et al*. 2018) but generalists may increase their activity (Massad *et al*. 2017). The degree of dissimilarity among individuals or species can be assumed to be functional for the survival of individuals or the persistence of species facing the assemblage of consumers predominant in their communities. However, that differentiation may not be enough to face plant consumers that did not evolve with a plant species, as in the case of *Ophiostoma novo-ulmi*, causal pathogen of the Dutch elm disease (Gibbs 1978, Brasier 1991). Also, the sensitivity of plant consumers to the differentiation among taxa may vary.

Summarizing the two previous sections: the α-, β-, and γ-phytochemical diversity are very high in ecosystems and landscapes; phytochemical diversity gets arranged in dynamic mosaics of mixtures of secondary metabolites that vary in their concentration and composition within (Robinson *et al*. 2022) and among individuals with particular chemical morphs in populations, species with unique chemical phenotypes, or in communities whose species differ in their array of phytochemical phenotypes (Defossez *et al*. 2021). The phytochemical mosaics select consumer species that can take advantage of them and exclude those that cannot. The degree of phytochemical differentiation among individuals and plant species is related to the susceptibility to herbivores and pathogens. Phytochemical diversity is fostered by evolutionary or coevolutionary processes, mainly under an arms-race scenario. Those processes are context-dependent, and their outcome depends on the species' identity and the local abiotic and biotic conditions.

Potential role of phytochemical diversity in agroecosystem management

In an agroecosystem, phytochemical diversity is structured by two interaction networks: the interactions between the domesticated crop and its associated agonists and antagonists, and the other by the interactions among the non-crop species adapted to that agroecosystem. The crop's network is structured by domestication-produced changes in the crop's morpho-physiology and phytochemistry that affect the crop's agonist and antagonist species and their natural enemies (Lindig-Cisneros *et al*. 1997, Benrey *et al*. 1998, Turlings & Wäckers 2004, Rasmann *et al*. 2005, Ode 2006, Kappers *et al*. 2011, Chen *et al*. 2015, Gaillard *et al*. 2018, Turlings & Erb 2018, Gasmi *et al*. 2019, Hauri *et al*. 2021). The non-crop species interaction network is constituted by the species that prosper in agroecosystems, such as microbes, arthropods, and weeds, which do not depend on the crop, although they may compete with the cultivated species. The complexity of those biotic interaction networks depends on their biodiversity, which is determined by the type of agriculture (traditional or industrialized) utilized. Therefore, to analyze which patterns or processes of phytochemical diversity in natural ecosystems might be helpful in agroecosystem management, we have to consider the effect of domestication on the phytochemical makeup of crops or semi-domesticated plants and the variability of agroecosystem types, as practices based on natural ecosystems might be fit only for some of them.

Traditional and industrial agroecosystems. Agroecosystems have very different characteristics depending on what type of agriculture fostered them. In one extreme, traditional agricultures produce many high-diversity agroecosystems, cultivating diverse crops adjusted to the local conditions (González Jácome 2021). There, the peasants continue a fine-tuning domestication process fostering the variability of crops and sowing selected seeds obtained in the agroecosystem for the following agricultural cycle. That implies that the crop's biotic interactions network mediated by PSM is both under artificial and natural selection. Additionally, the peasants use weeds and eliminate the undesired ones (Chacón & Gliessman 1982, Espinosa-García & Díaz-Pérez 1996, Vibrans 2016); also, the non-crop species may foster natural enemies to control pests and pathogens (Gliessman *et al.* 1998, Altieri & Nicholls 2004). Thus, the non-crop species are under artificial and natural selection adjusting all the biotic interactions in the agroecosystem to variable socioeconomic and environmental conditions.

On the other extreme, industrial agriculture produces high-yielding, low diversity agroecosystems adjusted to homogeneous monocultures grown in uniform conditions that exclude most non-crop species and pests and pathogens using pesticides; the crop seeds are purchased for every agricultural cycle from companies that continued the domestication process *ex situ* directed to increase yields and reduce costs by nullifying particular pests or abiotic factors (Bautista Lozada *et al.* 2012). Thus, the biotic interaction network for those crops is reduced to few insect pests, weeds, and pathogens, which evolve tolerance or resistance to pesticides, and crop mutualists that are introduced each cycle into the agroecosystem. The patterns or processes of phytochemical diversity in industrial agriculture favor an evolutionary analog of an arms-race scenario in which pests, weeds and pathogens adapt to pesticides or resistant crops and humans develop new pesticides or crop variants.

Therefore, the possible adaptation of the natural ecosystem phytochemical diversity patterns and processes to agroecosystems would vary in the traditional to industrial agroecosystem gradient. Traditional agroecosystems bear more resemblance to natural ecosystems than industrial ones; thus, many patterns and processes in which phytochemical diversity is involved may already operate in those agroecosystems.

For the industrial agroecosystems, the possibility of adapting natural ecosystems' patterns and processes is very low. However, some of those patterns and processes could be implemented by increasing biodiversity within and among crops, field parcels, and the landscape, thus increasing the chemical interactions implicit in biotic interactions (Valiente-Banuet *et al.* 2015, Sirami *et al.* 2019).

The complete reliance on phytochemical diversity to protect crops against pests and pathogens is very difficult, particularly in simplified agroecosystems occupying a large part of the landscape. Pests and pathogens thrive in large homogeneous monocultures with few weed species and impoverished soils. In those agroecosystems, pests and pathogens adapt to synthetic pesticides or the crop varieties resistant to single pests, and the crop antagonists move freely among individual plants and parcels. Thus, biological control should be implemented to suppress pests and pathogens, taking advantage of the volatiles emitted by crops (Peñaflor & Bento 2013).

Plant domestication and phytochemical diversity. Plant domestication occurs under artificial selection to favor traits that fulfill human needs, but natural selection continues operating on the plants under the domestication process eliminating the variants unable to survive after artificial selection in the human-intervened ecosystems. The domestication process may disrupt the coevolved biological interactions between the plants and their antagonists and agonists (Macfadyen & Bohan 2010) by changing and reducing the variability of morphological and phytochemical traits and the genetic makeup that were present in wild plants (Lindig-Cisneros *et al.* 1997, 2002, Blanckaert *et al.* 2012, Albores-Flores *et al.* 2018, Hernández-Cumplido *et al.* 2021). The type and degree of disruption vary depending on the domestication stage (Table 2), the life history of the crop, and the ecosystem where the domestication process occurs. For example, for perennial plants domesticated for their fruits *in situ* (that is, in or near the same ecosystem where the wild relatives occur) and that later could be planted in home gardens or rain-fed plots, the disruption can be minor (Casas *et al.* 2007, Avendaño-Gómez *et al.* 2015).

By contrast, in genetically engineered annual crops for monocultures in intensive agriculture, the disruption occurs in practically all the interaction networks in which their wild relatives participated (Macfadyen & Bohan 2010).

Table 2. Proposed stages of domestication according to the levels of intensity of change undergone by plant populations subject to human manipulation and domestication. Slightly modified from Clement (1999). There may be intermediate stages between two stages of domestication. Taken and translated from Bautista Lozada *et al*. (2012).

Domestication status	Population changes
Wild	Natural population whose phenotypes and genotypes have not been modified by human manipulation.
Evolution in systems under intensive human management	Species that grow in environments disturbed by humans, with possible genetic changes not produced by artificial selection (*e.g.*, weeds). In extreme cases some species only grow in these environments.
Incipient domestication	Human intervention at least by promotion (propagation) or tolerance in the system, but with the average phenotype of the selected trait still within the range of variation found in wild conditions. The variance of this average is possibly lower in populations managed under this stage and a reduction in genetic diversity begins to occur. This process occurs *in situ.*
Semi-domestication	Significant differences are evident with respect to wild populations due to human manipulation. The average and variance of the selected phenotype differ and increase, respectively, with respect to wild populations. The variance increases because phenotypes appear due to human manipulation that are not found in wild populations, and that will gradually disappear by natural selection in these populations. There is also a reduction in genetic diversity due to the bottleneck effect. Even so, the plant possesses ecological adaptability to reproduce and survive without depending on human care. This process occurs *in situ.*
Domestication	The plant is completely dependent on the agricultural environment and human care to survive and reproduce. Genetic diversity is usually significantly reduced and ecological adaptability is lost. However, when the domestication process occurs and continues in traditional agroecosystems, the crop's genetic variability is fostered by peasants.
Domestication for monoculture in simplified agroecosystems	The domestication process is carried out *ex-situ*, in laboratories, greenhouses, or experimental fields. The crop is completely dependent on simplified agroecosystems, synthetic agrochemicals and human care to survive and reproduce. Genetic diversity is null or highly reduced and ecological adaptability is lost.

The effect of domestication on the phytochemical diversity and the second and third trophic levels has been reviewed several times or subjected to meta-analysis (Bautista Lozada *et al*. 2012, Chen *et al*. 2015, Whitehead *et al*. 2017, Fernandez *et al*. 2021); the general agreement is that domestication favors herbivores and natural enemies by reducing chemical defense in the harvested parts of the crop but not necessarily in other plant parts. However, recent studies complicate understanding the effect of domestication on phytochemical defense. For example, low phytochemical diversity in monocultures may facilitate plant colonization by insect herbivores but hinder host localization by natural enemies; some compounds emitted after herbivore attack increase the susceptibility of some herbivores to insect pathogens, but other herbivores are not affected by those compounds (Gasmi *et al*. 2019); cucumber varieties differing in the quality of their emission of volatile mixtures attract generalist carnivore mites differentially (Kappers *et al*. 2011), but the genotypic variants of *Asclepias syriaca* emitted similar bouquets of volatiles after herbivore attack, but there, the amount of the mixture determined the natural enemies attack on the herbivore (Wason & Hunter 2014); mixtures of tomato cultivars with different odor chemotypes affected pest growth and survival, but hindered the hunt activity of predators (Hauri *et al*. 2021); domestication in tomato changed the volatile mixture emission in-

creasing the localization and colonization of the domesticated tomatoes by a specialist herbivore and decreasing the attraction of natural enemies (Li *et al*. 2018); and although domestication reduces most chemical defenses in maize, herbivory from generalists increases but herbivory from specialist herbivores decreases (Gaillard *et al*. 2018). The emerging pattern is that domestication reduces chemical defense concentration and the variability of the phytochemical mixtures, increasing herbivory mainly in the plant parts harvested by humans, but natural enemies frequently do not control herbivores. Generalist herbivores benefit from the phytochemical changes caused by domestication, but specialist herbivores do not always benefit from those changes. Those trends are more evident in annual crops than in tree crops, even the clonal ones.

Lessons from phytochemical diversity in natural ecosystems. The patterns or processes of phytochemical diversity in natural ecosystems are diverse and variable, mainly determined by biotic interactions and context-dependent; that is, idiosyncratic, because the evolutionary and ecological outcomes of the biotic interactions mediated by phytochemical diversity depend on the identity of the interacting species, the local ensemble of species and the local abiotic environment. Therefore, copying those natural ecosystem patterns and processes to agroecosystems is not viable, but adjustments can be made to get some resemblance. However, five recommendations based on ecosystem patterns and processes in which phytochemical diversity is involved could be helpful in agroecosystem management:

1.- The idiosyncratic nature of the outcomes where phytochemical diversity is involved implies that the responses to the phytochemical diversity of the species interacting with crops in an agroecosystem should be investigated case by case before deciding the best strategy to manage crop agonists and antagonists. That means that the sensitivity to the phytochemical mosaics of the agroecosystems should be investigated for the pest and mutualist species interacting with crops.

2.- Increasing phytochemical diversity at the individual, population, or community scale is desirable in agroecosystem management. However, the sole augmentation of diversity is not enough; the new phytochemical variants at those scales could be favorable to plant antagonists or disadvantageous for the crops and, therefore, eliminated by natural selection. Thus, the phytochemical variants that increase the plant fitness are the ones that should be considered an effective increase in phytochemical diversity.

3.- The phytochemical differentiation among crop individuals or cultivars at local agroecosystems should be investigated to be effective against local pests and pathogens. Also, the number of variants or varieties that will be intercropped should be investigated to prevent the evolution of devastating pests or pathogens. Homogeneous populations of plants with a low level of genetic variation, such as a field planted with an improved cereal cultivar, are assumed to be more susceptible to destruction by pests and pathogens (Pimentel & Bellotti 1976, Tooker & Frank 2012, Chaudhary 2013). The simultaneous cultivation of several cultivars with different resistance factors or cultivars with several genes for resistance to a pathogen or pest can avoid catastrophic attacks (Tooker & Frank 2012, McCarville *et al*. 2014). Although some of these strategies have worked for some annual crops (Borg *et al*. 2018, Tratwal & Bocianowski 2018, Grettenberger & Tooker 2020), phytochemical diversity is more important than cultivar diversity in pest and disease control (Hauri *et al*. 2021).

4.- The design of biopesticides based on phytochemical mixtures should avoid antagonistic interactions among their components and foster synergic interactions. Biopesticides based on a single PSM should be combined with other biopesticides as cocktails to prevent the evolution of resistance in pests and pathogens.

5.- The reduction in concentration and diversity in the chemical plant defense of crops suggests that effective pest control should include the recruitment of natural enemies to protect crops. The recruitment through volatile mixtures emitted by crops should be applied, excluding noxious phytochemicals for the natural enemies (Peñaflor & Bento 2013).

Concluding remarks

The patterns and processes in which phytochemical diversity is determinant are highly variable and context-dependent; moreover, the outcomes of those processes are determined by the identity of the species involved. Also, the function of phytochemical diversity is modulated by antagonist and agonist species that have evolved or coevolved with plants. Thus, copying those patterns and processes to industrial agroecosystems is challenging. However, in traditional agroecosystems, several (adjusted or resembling the originals) are already operating; therefore, there is no need to copy them. Instead, the principles supporting those patterns and processes in traditional agroecosystems could reduce the negative impacts of industrial agroecosystems. Still, some general principles derived from the structure and function of phytochemical diversity can be implemented in agroecosystems.

The knowledge of phytochemical diversity has increased rapidly since the advances in metabolomics and informatics; however, many research areas must be covered to disentangle the principles behind the extreme variability and diversity of plant secondary metabolites.

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