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Ecological evolutionary developmental biology in dialogue with agroecology

La ecología evolutiva del desarrollo en diálogo con la agroecología

Abstract | The fields of agroecology and ecological evolutionary developmental biology (eco–evo–devo) have been performing somewhat parallel efforts of synthesis. On the one hand, agroecology has incorporated knowledge from different disciplinary sources, among which are of course ecology, agronomy and, in a less extent, other scientific disciplines. It has also embraced local and traditional agricultural knowledge. On the other hand, during the last decades a large effort has aimed to integrate diverse theories, evidence and tools from ecology, developmental and evolutionary biology in what has been called eco–evo–devo. In this article we argue that these ongoing processes of synthesis can feedback each other with valuable theoretical and practical frameworks, as well as with questions and challenges that can push each other's borders. We conclude that the interaction between these two fields can provide a critical view of current conservation and agricultural policies and practices, for instance those related to germplasm conservation, and can help to tackle some of the open questions that are being addressed by the sciences, practices and social movements converging in agroecology.

Keywords | agroecology, ec–evo–devo, agrobiodiversity conservation, phenotypic plasticity, agricultural production

Resumen | Los campos de la agroecología y de la ecología evolutiva del desarrollo (eco–evo–devo) han llevado a cabo esfuerzos de síntesis que hasta ahora han avanzado en pa-

Recibido: 20 de julio de 2017. Aceptado: 16 de noviembre de 2017.

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I would like to thank members of the "Seminario de Agroecología y Domesticación" at CEIICH–UNAM, members of the laboratory "LaParcela" at LANCIS–IE–UNAM and members of "El Molote Agroecológico". I would also like to thank Naomi Nakayama for bringing to my attention the practice of *mugifumi*, and Emilio Mora, Irene Ramos and Lev Jardón Barbolla for their valuable comments on an earlier version of this work. This work has been supported by UNAM–DGAPA–PAPIIT (IA200714, IN113013-3) and CONACyT (221341, 247672).

Benítez, Mariana. «Ecological evolutionary developmental biology in dialogue with agroecology.» *Interdisciplina* 6, nº 14 (enero–abril 2018): 69-87.

DOI: http://dx.doi.org/10.22201/ceiich.24485705e.2018.14.63381

Volumen 6 | número 14 | enero–abril 2018
DOI: http://dx.doi.org/10.22201/ceiich.24485705e.2018.14.63381

ralelo. Por un lado, la agroecología ha incorporado el conocimiento de distintas fuentes disciplinares, entre las cuales están desde luego la ecología y la agronomía y, en menor medida, otras varias disciplinas científicas. La agroecología también ha incorporado parte del conocimiento agrícola tradicional. Por otro lado, durante las últimas décadas se han articulado diversas teorías, evidencia y herramientas de la ecología, la biología evolutiva y la biología del desarrollo en lo que se ha llamado eco–evo–devo. En este artículo argumentamos que estos dos procesos de síntesis pueden retroalimentarse desde sus valiosos marcos teóricos y prácticos, así como con preguntas y desafíos que lleven a empujar mutuamente las fronteras de la agroecología y del eco–evo–devo. Concluimos que la interacción entre estos dos campos puede proveer de una visión crítica hacia las estrategias de conservación y de producción agrícola, por ejemplo, de aquéllas relacionadas con la conservación del germoplasma, y que además puede ayudar a abordar algunas de las cuestiones que la agroecología trabaja en sus ejes de ciencia, práctica y movimiento social.
Palabras clave | agroecología, eco–evo–devo, conservación de la agrobiodiversidad, plasticidad fenotípica, producción agrícola

Agroecology
Sciences, practices and social movements

AGROECOLOGY IS an intrinsically transdisciplinary field. Not only does it feed from ecology, agronomy, anthropology, economy, among other disciplines, but it encompasses a set of practices and principles that have been developed in collaboration with organized peasants and small farmers. Indeed, agroecology is often understood along three axes: as a science, as a set of practical techniques and as a social movement vindicating the right to food sovereignty (Wezel *et al.* 2009; Sevilla–Guzmán and Woodgate 1997; Astier *et al.* 2017).

As a science emerging around 1930, agroecology aimed to understand cultivated plant systems as ecosystems, as well as to apply ecological concepts and methods to their study and improvement (Wezel *et al.* 2009). However, what is now identified as the agroecological practice may have its origins in some of the low–input millenarian forms of agriculture. Indeed, the interaction among the three axes mentioned above has led to a series of principles that go beyond academia and scientific practice. These principles, unlike the recipes or packages that are often promoted by the agroindustry, are adapted or further developed in local socio–ecological contexts, from which they continuously feed (Gliessman 1998; Altieri 1999).

Among the principles behind agroecology some are: i) to base its practice and technologies on the processes enabled by biodiversity, rather than on external, often oil–dependent inputs; ii) to foster productivity by using locally adapted plant varieties; iii) to pursue the local management of common resources and

the maintenance of local biogeochemical processes, instead of following extractive approaches; iv) to favor the recreation and reproduction of local biocultural heritage and to incorporate it into its practices and knowledge, and, v) to approach agroecosystems from an integrative, socio–ecosystemic view (Chappell 2013; Jardón Barbolla and Benítez 2016).

The objectives and ways of agroecology have recently been introduced to different academic and political contexts, and some of the key components of what we consider as agroecological science, practice and movement are at risk of being diluted or lost (Giraldo and Rosset 2016). Therefore, it is worth mentioning that we will consider Agroecology as inseparable from the notion of *food sovereignty*, which was coined by *La Vía Campesina* (the world's largest peasant organization), in 1996 to go beyond food security in asserting that the people who produce, distribute, and consume food should have the right to decide what they eat and the way food is produced and distributed (La Vía Campesina Website).[1]

Some open questions and challenges in Agroecology, an invitation to talk

Agroecology is currently a source of open questions and challenges that are pushing for a more integrative understanding of living beings, ecosystems and, specifically, of cultivated plant systems. In this section we put forward some of these questions and challenges.

In spite of its integrative nature, agroecology carries some limitations that might have been inherited from the disciplines that nurture it, biology in particular. Agroecology has adopted a critical position towards reductionist approaches to agriculture, deeply questioning the target–problem strategies (pests, soil limiting nutrient, etc.) and the emphasis on productivity of industrial agriculture (Altieri 1999; Lewontin and Levins 2007). It has also reacted to the analytical approach that has prevailed in many disciplines and favored an atomized and extremely specialized study of natural systems (Machado *et al*. 2009). Nevertheless, Agroecology has remained somewhat permeable to the so–called gene–centrism and the "hegemony of molecular biology" that have characterized Biology in the last century (Taylor and Lewontin 2017; Brigandt and Love 2017; Rheinberger *et al*. 2017). This refers to a type of reductionism considering genes as the main causal agent in the development and evolution of living organisms, and changes in gene sequences as the main source of variation.

For example, agroecology closely interacts with research programs on plant and animal domestication. Domestication has occurred in complex socio–eco-

1 https://viacampesina.org/en/food-sovereignty/, 2017.

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DOI: http://dx.doi.org/10.22201/ceiich.24485705e.2018.14.63381

logical contexts (e.g., Jardón Barbolla 2015), yet, in line with understanding evolution mainly as the change in allelic frequencies in a population (Taylor and Lewontin 2017), it is not uncommon to read about the genes for a given domestication–related trait. Genetic and population genetics approaches to the study of domestication are of course necessary and provide key evidence on the processes involved in domestication, but they contrast with the intricacies that characterize organism development and evolution, which go much beyond changes in allele frequency.

We will elaborate on this issue in the next section, but it is worth noting that a reduced view of domestication clearly affects the way in which agroecologists may conceptualize the *mode* and *tempo* of plant domestication, improvement and management, and the concomitant design of management practices. Indeed, the main focus of many agronomical and some agroecological efforts has been on maintaining and improving the *genetic resource*, while the physical and ecological aspects that contribute, along with the genetics of an organism, to phenotype formation have rarely been considered in the maintenance and improvement of whole–plant phenotypes (see examples for the importance of such non–genetic aspects below). As it will be discussed later on this text, the gene-centered and even the single–organism–based approach is insufficient to understand and intervene plant development and agroecosystem productivity and resilience, even more in rapidly changing environments.

On the other hand, current studies in agroecology are pushing for more integrative biological sciences. For instance, it has recently been uncovered that properties at the landscape scale can modify plant phenotypes at the single–plot scale (e.g., Chaplin–Kramer *et al.* 2011; Conelly *et al.* 2015). In particular, the spatial heterogeneity of the landscape and the type of human activities that take place in a given region can affect the development of plants inside a plot, which illustrates the active role that different scales of the environment can have on plant development, and eventually on the productivity of agroecosystems. Another example shows that the type of matrix surrounding coffee plantations affects the incidence of coffee pests on the cultivated plants: the incidence of the coffee rust, the most economically important coffee disease in the world, is clearly correlated with the proportion of pasture surrounding the coffee plots, probably because the low–wind–resistance in pasture lands favors the dispersion of the rust's spores (Avelino *et al.* 2012). How such multilevel interactions take place, on what temporal scale they affect plant phenotypes and yield, and how they impact ecosystem functions at the plot level are some of the questions that these and other findings pose to current biology in general.

Some of the ongoing agroecological strategies aiming to conserve or recover soil quality are based on processes involving whole biological communities and

organism–environment interactions. An example of this is the use of the so–called efficient or effective microorganisms, which are whole soil microbial communities incorporated to cultivated soils (Singh *et al*. 2011; Muñoz 2016). The use of this and other techniques is largely empirical and their understanding and further implementation or adaptation will certainly push the boundary of current knowledge in biological sciences.

Overall, in the context of social and environmental crises and rapid environmental changes, agroecology requires a deeper understanding of the biological and social processes that confer resilience to agroecosystems (Biggs *et al*. 2012). This is calling for a better understanding of the organism–environment interactions in developmental, ecological and evolutionary processes, as well as their response to different sources of environmental stress (Nicotra *et al*. 2010; de Ribou *et al*. 2013; Levis and Pfennig 2016; Turcotte and Levine 2016). Ideally, this knowledge could contribute to developing sustainable, locally adaptable and low–input strategies for food production, soil recovery and resilience.

Finally, the deep social roots of agroecology are motivating biological sciences, which have historically kept social factors apart from their research questions, to take into account the socio–ecological environment of living organisms. This might be the case of developmental and evolutionary biology (see below), which could greatly deepen its understanding of development and evolution when tackling questions such as: Do maize plants develop similarly in monoculture and in association with beans and squash, as maize has traditionally been grown in Mexico and Central America? Is the appearance and fixation of traits associated to domestication more likely in either of these two conditions? If so, what are the mechanisms behind this?

Ecological evolutionary developmental biology
An integrative effort in biological sciences

The recent integration of concepts, methods and interdisciplinary research from developmental biology and ecology into evolutionary theory has resulted in the emergence of ecological evolutionary developmental biology (eco–evo–devo) (Gilbert 2001; Abouheif *et al*. 2013; Gilbert *et al*. 2015). The main goal of this field is to uncover principles or mechanisms underlying the interactions between an organism's physical and ecological environment, genes, and development and to articulate such principles with evolutionary theory (Abouheif *et al*. 2013; Arias del Angel *et al*. 2015). Importantly, this integrative view acknowledges a variety of factors involved in the multi–causal development and evolution of organisms, going beyond the gene–centric approaches that were discussed before. It recognizes and attempts to understand the diversity in the

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sources of phenotypic variation (not only arising from genetic changes), as well as in the transgenerational inheritance of such variation (not only related to genetic inheritance).

As we will argue throughout this text, the concepts and methods bringing together development, ecology and evolution can function as contact points and help establish a powerful feedback with agroecology. This seems like a promising association in Latin America, where a vigorous community working on evo–devo and eco–evo–devo and many agroecological movements coincide (Brown *et al.* 2016; Altieri and Toledo 2011). We will focus on two of the key concepts of eco–evo–devo, although more of them could be abundantly discussed at the interface with agroecology (e.g., niche construction and developmental symbiosis; Gilbert *et al.* 2015; Levis and Pfennig 2016). These concepts are phenotypic and developmental plasticity and plasticity–first evolution.

Phenotypic plasticity can be understood as the output of an organism's development in its interaction with environment. When it is observed in embryonic or larval stages of plants and animals it is often called developmental plasticity (Gilbert and Epel 2015). Eco–evo–devo deals mostly with developmental plasticity, although the limits of its scope are blurred in cases in which development is indeterminate or exhibits intense post-embryonic manifestations, as it does in plants. While plasticity is often used to refer to changes in an organism's behavior, morphology and physiology in response to its environment, we consider it emphasizes the active role of environment on the generation of phenotypes. Indeed, rather than the organism *responding* to an environment, it seems more accurate to think of the development of an organism as the interpenetration of genetic, environmental and physicochemical processes acting in conjunction (Lewontin 2001; Newman 2012; Arias del Angel *et al.* 2015; among many others).

Phenotypic and developmental plasticity can be illustrated by countless examples in different taxa. For instance, the same plant population can develop completely different leaves depending on whether plants develop below or above water, or can modify the size and architecture of its roots depending on nutrient availability and other soil conditions. This phenomenon has also been studied in some plants of agricultural interest (e.g., Mercer and Perales 2010). Indeed, the role of physico–chemical, ecological and even the social environment (e.g., plant management practices) is a constructive one. This is qualitatively different from thinking of the environment as a source of noise and deviations from an hypothetical norm.

A valuable tool to study and characterize phenotypic plasticity is the reaction norm, which describes the pattern of phenotypic expression for a single genotype in an environmental gradient. Reaction norms thus help visualize and measure the way organisms change their morphology, behavior or physiology

when they develop in different environmental conditions. Reaction norm experiments have shown that plasticity may not always lead to adaptive phenotypes and that plastic changes might exhibit different patterns for different environmental factors (e.g., temperature, nutrient and water availability, etc.) (Vía *et al.* 1995), and even for different organs or traits of the same individuals (e.g., leaf number, leaf size, trichome density; Ojeda Linares 2017).

It is worth noting that, while plasticity studies and reaction norm analyses draw on quantitative genetics, eco–evo–devo has added an explicit focus on the genetic, cellular and organismal mechanisms that interact with the environment, bringing ecological causes and a process–based view to the heart of developmental and plasticity studies (Sultan 2007; Gilbert and Epel 2015). Eco–evo–devo has also emphasized the role of plastic development in evolution, so much so that this view has been argued to be part of an *extended evolutionary synthesis* (Pigliucci and Müller 2010).

Biological evolution requires phenotypic variation, since it is on the basis of non-neutral variation that novel phenotyes might be selected and fixed in populations. A current avenue of active research in eco–evo–devo involves the question of whether phenotypic variation generated by plasticity can precede or facilitate evolutionary change. This question has remained controversial because the modern evolutionary synthesis considers genetic change, mainly genetic mutations, as the most relevant source of variation in biological populations. However, theory and growing empirical evidence show that plasticity–first evolution is possible and suggest that it might be important in natural populations (West–Eberhard 2013; Jablonka and Lamb 2014; Gilbert *et al.* 2015; Levis and Pfennig 2016).

The proposed mechanisms behind plasticity–first evolution are more than one and are explained elsewhere in detail (e.g., Schmalhausen 1949; Waddington 1942; West–Eberhard 2003; Müller and Pigliucci 2010), but one of them could be simplified in the following steps: a phenotypic variant arises in a population in a given environmental condition due to phenotypic plasticity; if this novel phenotype is relatively fit to the environment, organisms with such phenotype will survive and reproduce; if the last step occurs for several generations, the random genetic mutations that occur in the populations are more likely to be maintained in the population if they allow or favor the development of the fit environmentally–induced phenotypes. Eventually, this leads to a population in which the phenotype that was initially generated in a given environment becomes *genetically assimilated* (Waddington 1942) and persists by means of genetic inheritance in the population, even if the environmental conditions change.

Interestingly, this type of process could be accelerated or reinforced by extragenic inheritance, this is, inheritance that can occur owing to diverse molecular, ecological and social processes that do not involve genetic inheritance

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(Agrawal 2002; Jablonka and Raz 2009; Susuky and Nijhout 2006; Herman and Sultan 2002). In this scenario, the evolution of adaptive phenotypes might occur faster than it is usually thought, which would be consistent with some of the rapid events of diversification reported in plant domestication processes.

Open questions and provocations from and to the eco–evo–devo side

As it is the case in Agroecological research, there are current challenges and open questions in eco–evo–devo that could stimulate the dialogue between these two fields. The questions that we will consider here are mostly related to the role of plasticity in the ecological and evolutionary dimensions of organismal development.

A recent meta–analysis shows that approximately one fourth of the total trait variation within plant communities is due to variation within species (Siefert *et al*. 2015). Given the low average heritability reported in this meta–analysis for this type of variation, it is likely to largely correspond to phenotypic plasticity (Siefert *et al*. 2015). How plastic variation affects or drives ecological dynamics and evolution, in particular the potential coexistence of species in an ecological community, remains an open question. Actually, there is contradictory evidence as to whether plasticity promotes or hinders species coexistence. In any case, it has been proposed that plasticity plays a major role in the assembly and resilience of ecological communities (Turcotte *et al*. 2016). Of special interest in an scenario of climate change, is understanding whether plasticity is likely to promote species coexistence in variable environments. A particular instance of this question will be understanding the effect of plasticity in the potential coexistence or competition among native and potentially invasive species, which are likely to extend their distribution given to changes in environmental conditions (Strauss *et al*. 2006; Hulme 2008).

One of the challenges in testing for plasticity–first evolution is finding suitable study systems in natural populations (Levis and Pfennig 2016). These systems should, among other things, help answer how fast real populations can evolve in complex socio–ecological contexts, as well as what are the socio–ecological conditions that enable, drive or enhance this type of evolution. Specifically, current experimental explorations of plasticity are mostly performed for single species isolated in the laboratory or in a greenhouse, and there is a pressing need to develop experimental settings in multispecies contexts.

Similarly, many of the processes involved in the expression and evolution of plasticity have been described in model organisms in laboratory or greenhouse conditions, going from the classical experiments of C.H. Waddington with

fruit flies to the ongoing studies in a few other animal and plant species (e.g., Suzuki and Nijhout 2006). It is thus worth asking if non–model organisms exhibit some of the phenomena that have been reported for model ones. Indeed, it seems that model organisms may carry or share traits —some of which make them good laboratory systems— that do not reflect the behavior or features of the vast majority of plants and animals (Jenner *et al.* 2007; Gilbert 2009).

Another open question in eco–evo–devo is what the conditions that select or favor the evolution of plasticity are. Answering this question will require joint theoretical and experimental approaches (e.g., Wagner 1996; Ojeda Linares 2017), but could greatly benefit from the establishment of long–term systems for the study of plasticity under different climatic, ecological and social conditions.

Finally, it has been convincingly argued that science in general benefits from widening its scope of sources of knowledge and evidence (e.g., Levins 2015). This implies that research steps outside academia to incorporate, in a rigorous way, other knowledge and worldviews. In the case of eco–evo–devo, this would require asking what local knowledge and practices can teach this field. This is of special importance in man–made or intervened environments, which nowadays occupy the majority of the surface of the planet.

For instance, there is a Japanese agricultural practice known as mugifumi, which consists on the mechanical stimulation of the seedlings of wheat and barley by treading. As 17th century sources confirm, Japanese farmers have known for centuries that treading prevents spindly growth, strengthens the roots, increases tillers and ear length, and eventually increases yield (Iida 2014). Coincidently, one of the current avenues in developmental biology is that of studying the interactions among mechanical, genetic and hormonal factors during plant growth, as well as the macroscopic effects of such interactions (Newman 2012; Hammant 2017).

In a bidirectional interaction between academia and other social actors, it is also necessary to ask how knowledge and research in eco–evo–devo can back social movements towards food sovereignty, social and environmental justice, and sustainability. So far, research in eco–evo–devo has already accompanied or advised some social struggles to conserve cultural and biological diversity (various chapters in Alvarez–Buylla and Piñeyro 2014).

Towards more integrative sciences, practices and movements

Potential model systems to address agroecological and eco–evo–devo research questions

In this section we will comment on potential feedback interactions between Agroecology and eco–evo–devo, in particular in setting up common model sys-

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tems. To this end, we will consider phenotypic plasticity and multiscale, multispecies interactions as possible contact points.

In spite of plasticity's importance as a cause for ecologically and evolutionary relevant variation (almost any biologist will acknowledge the prevalence and significance of plasticity), it has often been treated as a nuance and has not usually been considered in experimental designs or research questions (Robert 2002; although see examples of exceptions in Schlichting and Pigliucci 1998; and West–Eberhard 2003; Gremillion and Piperno 2009). Actually, most developmental studies carried out in the last decades have tried to keep environmental conditions fixed to then uncover the genetic changes that are supposed to determine phenotypes and their variation (Robert 2004). Work on the complementary way is needed, assessing and integrating physico–chemical and socio–ecological factors into the conceptual and experimental models for organismal development.

Agroecosystems provide a great setting to study phenotypic plasticity and eco–evo–devo questions. In particular, traditional agroecosystems constitute invaluable model systems. First, these systems are often practiced as polycultures in thousands or millions of plots in diverse environmental conditions (e.g., maize cultivation in Mexico ranges from 0 mamsl to more than 2200 mamsl; see relevant work by Mercer and Perales 2010), which allows to pursue the analysis of vast and heterogeneous data outside laboratories, beyond classical model organisms, and in multispecies scenarios. Second, the techniques, traditions and practices associated to the management of traditional agroecosystems reflect deep ecological knowledge (Boege 2008; Levins 2015), and there is often a socially–distributed knowledge of the history and characteristics of each plot. Third, the complexity of these systems, which certainly challenges the standard protocols in eco–evo–devo, can help us correct and complement the way we understand interactions among genetic, cellular, ecological, physico–chemical and social factors, ranging from the microscopic scale of soil bacteria consortia to the regional scale of ecological landscapes.

On the side of the agroecological sciences, practices and social movements, the knowledge that eco–evo–devo can provide about the diverse processes involved in plant domestication and breeding can inform the in–field practices for plant management, as well as for seed selection and conservation. Moreover, integrative research in biological sciences can allow to explore questions such as: i) the effect of multiple ecological interactions (e.g., bacteria–plant–pollinator) on the response of cultivated plants to environmental stress along one or more plant generations; ii) the effect of multiscale ecological interactions on the yield, resilience and vulnerability of agroecosystems; how does land use around a plot affect cultivated plants inside the plot?, how can a group of producers or-

ganize to configure their shared territory as best as possible in terms of agroecosystemic yield and resilience?, and, iii) the genetic, social and environmental conditions that favor the plastic and adaptive response of plants and of the whole agroecosystems in the face of different perturbations.

The *milpa*, an example of traditional agroecosystems, is a potential model system to pursue the questions mentioned above. This system has been practiced as a polyculture of maize, common bean and other cultivated and associated plants for thousands of years in the Mesoamerican region. The milpa is at the core of food sovereignty struggles in Latin America (Boege 2008; Chappell *et al*. 2013) and, since it has been practiced over a vast range of environmental and cultural conditions, this agroecosystem is recognized as an important repository of biological and cultural diversity (Boege *et al*. 2008). It is in the context of this peasant laboratory that thousands of varieties of maize, bean, squash, tomato, chili pepper, among other plants, have been evolved (Boege 2008). It seems only natural to learn from the adaptability of these varieties and multispecies associations about plant ecological evolutionary development, and about ways to face rapid environmental and social changes.

There is some ongoing work on the directions sketched here. In particular, a project based at Mexico's National University is aiming to study the biological and social processes behind the great diversity of domesticated varieties of chili pepper (Jardón Barbolla 2017). This plant, which has been domesticated in diverse cultural and environmental contexts, offers the opportunity to articulate some of the theoretical and practical tools of agroecology and eco–evo–devo to understand how phenotypic variation is distributed along soil, climatic and management gradients, or how peasant selection for certain cultural uses of chili pepper has affected genetic and phenotypic diversity.

An integrative perspective on problems and strategies for conservation and food production

As mentioned above, most of the extant agrobiodiversity has been generated in traditional agroecosystems by intricate developmental, ecological, evolutionary and social processes. Moreover, this agrobiodiversity is part of the biocultural heritage of millions of small farmers and peasants around the world, who in turn recreate their identity and culture around such diversity of domesticated plants and animals (Boege 2008; CEMDA 2016). However, diverse political and economical pressures, often reflected in agricultural policies and programs fostering monoculture and input-dependent agriculture, have led to the loss or near extinction of thousands of varieties around the world. About 75 percent of plant genetic diversity has been lost as local varieties and landraces and has

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been substituted by genetically uniform varieties (FAO Agrobiodiversity Website 2017); just as an example, from the more than 500 varieties of cabbage commercially available at the beginning of the twentieth century, only around 30 were commercially available by the end of the same century (RAFI 2014).

This in turn leads to the loss of an incommensurable amount of non–cultivated plants, livestock and wild species that are associated to these varieties and whose temporary or permanent establishment is allowed only in certain types of agriculture (FAO Website for Agrobiodiversity 2017; Perfecto *et al*. 2009). The risk of losing native varieties is worsened, and largely caused, by the extremely vulnerable conditions in which rural communities live in most of the world, which leads to migration, abandonment of agriculture and deterioration of the socio–ecosystemic processes that have rendered and continue to create locally adapted varieties (Chappell *et al*. 2013).

In the context of such agrobiodiversity crisis, different strategies have been adopted by different sectors of the society. On the one hand, several governments and corporations have favored the establishment of large, highly secured seed and germplasm banks that aim to protect the existing seeds in the case of catastrophes or global crises (see Svalbard Global Seed Vault Website). While this type of effort might be necessary, depending on who has access to the secured diversity, this approach is largely insufficient, as it can be argued both from the agroecological and eco–evo–devo perspectives sketched above.

Since the seeds and germplasm are by definition the carriers of the genetic information of a given organism, it is plausible from a gene–centric view to conserve the varieties and species of interest from their seeds or germplasm. However, rather than copied or decoded from their genetic information, organisms are *recreated* generation after generation during development by the interaction among their genetic processes, their ecological interactions and, in the case of agroecosystems, man–made environments, social and cultural practices. Actually, one of the sociocultural practices that has led to the currently existing agrobiodiversity is the informal and constant seed exchange that farmers and peasants have practiced all over the world. This practice, among others, is at risk of becoming illegal in tens of countries by the similarly limited view reflected by the international tools that allegedly pursue the protection of new plant varieties (UPOV Website 2017; Jardon Barbolla 2015; La Vía Campesina Website).

It results thus limited to aim only at the conservation of germplasm of varieties whose cultivation and use rely on local techniques and knowledge that, if not practiced or not meaningful, are lost. It could be said that seed and germplasm bank strategies aim to save a hypothetical essence of the desired species and varieties —an essence questionably deposited on the genes—, rather than guaran-

tee that the processes and livelihoods that have generated them, and that could generate many more, can continue to occur (Jardón Barbolla and Benítez 2016).

In contrast with these conservation strategies, peasant movements in the world refuse to keep our biocultural heritage in museums and banks, and aim to guaranteeing the conditions that allow peasants to live with dignity and to continue to take part in the evolutionary processes that have created agrobiodiversity. In its social axis, agroecology has incorporated and designed diverse social practices and techniques that allow for collaborative learning and experimentation among peasants, students, technicians and researches, and that can sometimes be more useful in the process of building food sovereignty than the agroecological techniques themselves (P. Rossett in Escuela Campesina Multimedia).[2]

The "campesino to campesino" and "participatory action research" frameworks are good examples of such approach and involve a set of well–described principles and techniques (workshops, research protocols, social organization schemes, etcetera) that could guide work in different agricultural contexts (Escuela Campesina Multimedia,[3] Rosset *et al.* 2001; Holt–Jimenez 2006; Méndez *et al.* 2013). From an agroecological and eco–evo–devo perspective, this transdisciplinary approach seems much more suitable to fostering the processes that have created agrobiodiversity than the conservation proposals described before. Indeed this type of approach has enhanced the conservation and further adaptation of agrobiodiversity by maintaining or generating a distributed system of learning, experimentation and production that does not depend, or tends to depend less and less, from centralized sources of inputs (machinery, synthetic agrochemicals and even seeds) and knowledge (state or private technicians). In this context, communitary seed and germplasm banks are key, but are just part of a net of practices that reinforce each other to guarantee the recreation of cultural and biological diversity (Holt–Giménez 2006).

Agroecology and eco–evo–devo have and can learn from this scenario more than it might seem at first sight. Performing scientific research in collaboration with organized groups of producers can entail a degree of freedom and possibilities that are ever more unusual in the academic context. It becomes possible in this context, for example, to perform large–scale and long–term experiments that are also of interest for the producers, and that might be extremely difficult to pursue via the standard academic avenues. Local knowledge, needs and questions have nurtured agroecology and could enrich eco–evo–devo research in valuable and unexpected ways.

2 http://agroecologia.espora.org/general-introduction/
3 http://agroecologia.espora.org/general-introduction/

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In the face of the current crisis of biodiversity and agrobiodiversity loss, climate change and persisting hunger, it might seem that the "simple" methods to guarantee food sovereignty have already been applied and that new technological developments and ever more secure seed banks are the only way to follow. Nevertheless, considering the lessons learned from eco–evo–devo and agroecology, as well as the overwhelming fact that around 70% of the food humans consume is produced by small farmers and peasants, who have access to 30% of the land and water resources (ETC Group 2009), it seems more reasonable to bet on small–farmer and campesino agriculture to maintain and increase agrobiodiversity. It is only fair to join the struggle of millions of peasants to guarantee that traditional agroecosystems, agrobiodiversity and whole livelihoods and cultures can be ecologically and socially reproduced in a context of food sovereignty (Chappell *et al*. 2013; CEMDA 2016). One way of supporting this struggle is to further the shared and integrative knowledge on agroecosystems.

References

Abouheif, E., Favé, M. J., Ibarrarán–Viniegra, A. S., Lesoway, M. P., Rafiqi, A. M. and Rajakumar, R. «Eco–evo–devo: The time has come.» *Ecological genomics*. Netherlands: Springer, 107-125, 2014.

Agrawal, A. A. «Herbivory and maternal effects: Mechanisms and consequences of transgenerational induced plant resistance.» *Ecology*, 83(12), 3408-3415, 2002.

Altieri, M. A. H., Liebman, S., Magdoff, M., Norgaard, F., Sikor, R. and Thomas, O. *Agroecología: Bases científicas para una agricultura sustentable*. Nordan–Comunidad, 1999.

——— and Toledo, V. M. «The agroecological revolution in Latin America: Rescuing nature, ensuring food sovereignty and empowering peasants.» J*ournal of Peasant Studies*, 38(3): 587-612, 2011.

Alvarez–Buylla, E. and Piñeyro, A. *El maíz en peligro ante los transgénicos*. México: CEIICH–UNAM, 2014.

Arias del Angel J. A., Azpeitia E., Benítez M., Escalante A. E., Hernández–Hernández V., Mora van Cauwelaert E. «Physicochemical factors in the organization of multicellular aggregates and plants.» In K. Niklas, S. A. Newman (eds.), *The origin and consequences of multicellularity*. The Vienna Seeries on Theoretical Biology, MIT Press, 2015.

Astier, M., Argueta, J. Q., Orozco–Ramírez, Q., González, M. V., Morales, J., Gerritsen, P. R., ... and Sánchez–Sánchez, C. «Back to the roots: Understanding current agroecological movement, science, and practice in Mexico.» *Agroecology and Sustainable Food Systems*, 41(3-4): 329-348, 2017.

Biggs, R., Schlüter, M., Biggs, D., Bohensky, E. L., BurnSilver, S., Cundill, G., ... and Leitch, A. M. «Toward principles for enhancing the resilience of ecosystem services.» *Annual review of environment and resources*, 37: 421-448, 2012.

Brigandt, I., Love, A. «Reductionism in biology.» In Edward N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2017 Edition), https://plato.stanford.edu/archives/spr2017/entries/reduction-biology/

Boege, E. *El patrimonio biocultural de los pueblos indígenas de México: hacia la conservación in situ de la biodiversidad y agrodiversidad en los territorios indígenas*, 2008 (No. Sirsi) (i97896803854).

CEMDA, Centro Mexicano de Derecho Ambiental. Informe sobre la pertinencia biocultural de la legislación mexicana y su política pública para el campo: el caso del programa de "Modernización Sustentable de la Agricultura Tradicional". 2016. (MasAgro): http://www.cemda.org.mx/wpcontent/uploads/2016/12/InformeMasAgro.pdf

Chaplin–Kramer, R., O'Rourke, M. E., Blitzer, E. J. and Kremen, C. «A meta-analysis of crop pest and natural enemy response to landscape complexity.» *Ecology letters*,14(9): 922-932, 2011.

Chappell, M. J., Wittman, H., Bacon, C. M., Ferguson, B. G., Barrios, L. G., Barrios, R. G., ... and Soto–Pinto, L. «Food sovereignty: An alternative paradigm for poverty reduction and biodiversity conservation in Latin America.» *F1000Research*, 2, 2013.

Chautá–Mellizo, A., Campbell, S. A., Bonilla, M. A., Thaler, J. S. and Poveda, K. «Effects of natural and artificial pollination on fruit and offspring quality.» *Basic and applied ecology*, 13(6): 524-532, 2012.

Connelly, H., Poveda, K. and Loeb, G. «Landscape simplification decreases wild bee pollination services to strawberry.» *Agriculture, Ecosystems and Environment*, 211: 51-56, 2015.

De Ribou, S. D. B., Douam, F., Hamant, O., Frohlich, M. W. and Negrutiu, I. «Plant science and agricultural productivity: Why are we hitting the yield ceiling?» *Plant Science*, 210: 159-176, 2013.

ETC Group. *Who will feed us?*, 2009. http://www.etcgroup.org/content/who-will-feed-us.

FAO Website for Agrobiodiversity: www.fao.org/biodiversity/index.asp?lang=en (Consulted in July, 2017).

Gilbert, S. F. «The adequacy of model systems for evo-devo: Modeling the formation of organisms/modeling the formation of society.» In Barberousse, Morange, Pradeu (eds.), *Mapping the future of biology*, 57-68. 2009. ISBN: 978-1-4020-9635-8 (Print) 978-1-4020-9636-5 (Online).

——— and Epel, D. *Ecological developmental biology: The environmental regula-*

Volumen 6 | número 14 | enero–abril 2018
DOI: http://dx.doi.org/10.22201/ceiich.24485705e.2018.14.63381

tion of development, health, and evolution. Sinauer Associates, Incorporated Publishers, 2015.

——— «Ecological developmental biology: Developmental biology meets the real world.» *Developmental biology*, 233(1): 1-12, 2001.

———, Bosch, T. C. and Ledón–Rettig, C. «Eco–evo–devo: Developmental symbiosis and developmental plasticity as evolutionary agents.» *Nature Reviews Genetics*, 16(10), 611-622, 2015.

Giraldo, O. F., Rosset, P. «La agroecología en una encrucijada: entre la institucionalidad y los movimientos sociales.» *Guaju–Revista Brasileira de Desenvolvimento Territorial Sustentável*, 2(1): 14-37, 2016.

Gliessman, S. R., Engles, E. and Krieger, R. *Agroecology: Ecological processes in sustainable agriculture*. CRC Press, 1998.

Gremillion, K. J. and Piperno, D. R. «Human behavioral ecology, phenotypic (developmental) plasticity, and agricultural origins: Insights from the emerging evolutionary synthesis.» *Current Anthropology*, 50(5): 615-619, 2009.

Hamant, O. «Mechano–devo.» *Mechanisms of Development*, 147: 2-9, June, 2017.

Herman, J. J. and Sultan, S. E. «Adaptive transgenerational plasticity in plants: Case studies, mechanisms, and implications for natural populations.» *Frontiers in Plant Science*, 2: 102. doi: 10.3389/fpls.2011.00102.

Holt–Giménez, E. *Campesino a campesino: Voices from Latin America's farmer to farmer movement for sustainable agriculture*. Food First Books, 2006.

Hulme, P. E. «Phenotypic plasticity and plant invasions: Is it all Jack?» *Functional Ecology*, 22(1): 3-7, 2008.

Iida, H. «Mugifumi, a beneficial farm work of adding mechanical stress by treading to wheat and barley seedlings.» *Frontiers in Plant Science*, 5, 2014.

Jablonka, E. and Lamb, M. J. *Evolution in four dimensions, revised edition: Genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT press, 2014.

——— and Raz, G. «Transgenerational epigenetic inheritance: Prevalence, mechanisms, and implications for the study of heredity and evolution.» *The Quarterly review of biology*, 84(2): 131-176, 2009.

Jardón Barbolla, L. (2015). «De la evolución al valor de uso, ida y vuelta: exploraciones en la domesticación y diversificación de plantas.» *INTERdisciplina*, 3(5), 2015.

——— «De Sonora a Yucatán. Chiles en México: diversidad y domesticación.» *OIKOS*=, 17: 25-30, 2017.

———, L. and Benítez, M. «La comunidad agroecológica como unidad ecológica, de domesticación y de conservación.» In Guerrero McManus, Valadez Blanco, Vizcaya Xilotl (eds.), *Naturaleza, ciencia y sociedad*, Copit–Arxives, 206, CdMx. ISBN: 9781938128127.

Jenner, R. A. and Wills, M. A. «The choice of model organisms in evo–devo.» *Nature Reviews Genetics*, 8(4): 311-314, 2017.

Latimer, J. G. «Mechanical conditioning for control of growth and quality of vegetable transplants.» *Hort Science*, 26(12): 1456-1461, 1991.

Levins, R. *Una pierna adentro, una pierna afuera*. México: CopIt ArXives and EditoraC3, 2015. SC0005ES. ISBN: 978-1-938128-07-3.

Levis, N. A. and Pfennig, D. W. «Evaluating 'plasticity-first'evolution in nature: Key criteria and empirical approaches.» *Trends in ecology and evolution*, 31(7): 563-574, 2016.

Lewontin, R. and Levins, R. *Biology under the influence: Dialectical essays on the coevolution of nature and society*. NYU Press, 2007.

Machado, H., Suset, A., Martín, G. J. and Funes–Monzote, F. R. «From the reductionist approach to the system approach in Cuban agriculture: A necessary change of vision.» *Pastos y Forrajes*, 32(3): 215-235, 2009.

Marcellini, S., González, F., Sarrazin, A. F., Pabón–Mroa, N., Benítez, M., Piñeyro–Nelson, A. ... and Da Fonseca, R. N. «Evolutionary developmental biology (evo–devo) research in Latin America.» *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, 328(1-2): 5-40, 2016.

Méndez, V. E., Bacon, C. M. and Cohen, R. «Agroecology as a transdisciplinary, participatory, and action-oriented approach.» *Agroecology and Sustainable Food Systems*, 37(1), 3-18, 2013.

Mercer, K. L. and Perales, H. R. «Evolutionary response of landraces to climate change in centers of crop diversity.» *Evolutionary applications*, 3(5-6), 480-493, 2010.

Muñoz, C. R. R. «Impacto del curso los microorganismos eficientes y su uso en la agricultura en docentes de especialidades agropecuarias, provincia Cienfuegos.» *Revista Conrado*, 12(55), 2016.

Newman, S. A. Physico–genetic determinants in the evolution of development. *Science*, 338(6104): 217-219, 2012.

Nicotra, A. B., Atkin, O. K., Bonser, S. P., Davidson, A. M., Finnegan, E. J., Mathesius, U. ... and Van Kleunen, M. «Plant phenotypic plasticity in a changing climate.» *Trends in plant science*, 15(12), 684-692, 2010.

Ojeda Linares, C.I. *Evaluación de la variabilidad morfológica de las hojas de* Arabidopsis thaliana *como identificador de la plasticidad fenotípica de distintos ecotipos*. Tesis para obtener el grado de maestría en ciencias biológicas, Universidad Nacional Autónoma de México. 2017.

Pigliucci, M. and Müller, G. *Evolution, the extended synthesis*. MIT Press, 2010. ISBN-13: 978-0262513678.

Rheinberger, Hans–Jörg, Müller–Wille, Staffan and Meunier, Robert. «Gene.» In Edward N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Spring 2015

Volumen 6 | número 14 | enero–abril 2018
DOI: http://dx.doi.org/10.22201/ceiich.24485705e.2018.14.63381

Edition), https://plato.stanford.edu/archives/spr2015/entries/gene/

RAFI, Rural Advancement Foundation International. *Vegetable variety inventory: Varieties from USDA 1903 list of American vegetables, in storage at the national seed storage library*. 1983.

Robert, J. S. *Embryology, epigenesis and evolution: Taking development seriously*. Cambridge University Press, 2004.

Rosset, P. M., Machín Sosa, B., Roque Jaime, A. M. and Ávila Lozano, D. R. «The campesino–to–campesino agroecology movement of ANAP in Cuba: Social process methodology in the construction of sustainable peasant agriculture and food sovereignty.» *The Journal of peasant studies*, 38(1): 161-191, 2011.

Schlichting, C. D. and Pigliucci, M. *Phenotypic evolution: A reaction norm perspective*. Sinauer Associates Incorporated, 1998.

Schmalhausen, I. I. *Factors of evolution: The theory of stabilizing selection*, 1949.

Sevilla–Guzmán, E. y G. Woodgate. «'Sustainable rural development': From industrial agriculture to agroecology.» In M. Redclift y G. Woodgate (eds.), *The international handbook of environmental sociology*, first ed. Cheltenham: Edward Elgar, 83-100, 1997.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A. ... and L. Dantas, V. «A global meta–analysis of the relative extent of intraspecific trait variation in plant communities.» *Ecology Letters*, 18(12): 1406-1419, 2015.

Singh, J. S., Pandey, V. C. and Singh, D. P. «Efficient soil microorganisms: A new dimension for sustainable agriculture and environmental development.» *Agriculture, ecosystems and environment*, 140(3): 339-353, 2011.

Strauss, S. Y., Lau, J. A. and Carroll, S. P. «Evolutionary responses of natives to introduced species: What do introductions tell us about natural communities?» *Ecology letters*, 9(3): 357-374, 2006.

Sultan, S. E. «Development in context: The timely emergence of eco–devo.» *Trends in Ecology & Evolution*, 22(11): 575-582, 2007.

Suzuki, Y. and Nijhout, H. F. «Evolution of a polyphenism by genetic accommodation.» *Science*, 311(5761): 650-652, 2006.

Taylor, Peter and Lewontin, Richard. «The genotype/phenotype distinction.» In Edward N. Zalta (ed.), *The Stanford Encyclopedia of Philosophy* (Summer 2017 edition). https://plato.stanford.edu/archives/sum2017/entries/genotype-phenotype/

Turcotte, M. M. and Levine, J. M. «Phenotypic plasticity and species coexistence.» *Trends in ecology and evolution*, 31(10): 803-813, 2016.

UPOV Website. International Convention for the Protection of New Varieties of Plants (Consulted in July, 2017). http://www.upov.int/upovlex/en/conventions/1978/act1978.html

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D. and Van

Tienderen, P. H. «Adaptive phenotypic plasticity: Consensus and controversy.» *Trends in Ecology and Evolution*, 10(5): 212-217, 1995.

Waddington, C. H. «Canalization of development and the inheritance of acquired characters.» *Nature*, 150(3811): 563-565, 1942.

Wagner, A. «Does evolutionary plasticity evolve?» *Evolution*, 50(3): 1008-1023, 1996.

Wezel, A., Bellon, S., Doré, T., Francis, C., Vallod, D. and David, C. «Agroecology as a science, a movement and a practice. A review.» *Agronomy for Sustainable Development*, 29(4): 503-515, 2009.

West–Eberhard, M. J. *Developmental plasticity and evolution*. Oxford University Press, 2003.