

Approaching the domesticated plant holobiont from a community evolution perspective

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Abstract

Plants establish a pivotal relationship with their microbiome and are often conceptualized as holobionts. Nonetheless, holobiont theories have attracted much criticism, especially concerning the fact that the holobiont is rarely a unit of selection. In previous work, we discussed how the plant microbiome can be considered to be an 'ecosystem on a leash', which is subject to the influence of natural selection acting on plant traits. We proposed that in domesticated plants the assembly of the plant microbiome can usefully be conceptualized as being subject to a 'double leash', which encompasses both the effect of artificial selection imposed by the domesticator on plant traits and the leash from the plant to the microbiome. Here we approach the domesticated plant holobiont, simply defined as a community of organisms, from a community evolution point of view, and show how community heritability (a measure of community selection) complements the 'double-leash' framework in providing a community-level view of plant domestication and its impact on plant-microbe interactions. We also propose simple experiments that could be performed to investigate whether plant domestication has altered the potential for community selection at the holobiont level.

INTRODUCTION

In recent years, we have come to appreciate that as single individuals can have heritable phenotypes, the effect of these phenotypes on a community or at ecosystem level can also lead to heritable community and ecosystem phenotypes [1]. Because micro-organisms are ubiquitous in virtually all environments on Earth, plant and animal species do not evolve in isolation but are colonized by a rich and diverse microbial community [2]. Therefore, the effect of a heritable host phenotype can lead to a heritable component of the host microbiome. Potentially, the host and its microbiome, a holobiont, can be subject to community selection, which may lead to community evolution [3]. Community evolution is the 'outcome of selection operating at multiple levels that results in the differential survival and proliferation of communities' [4]. Through community evolution, specific microbial community phenotypes could arise, which may provide positive microbe-to-host effects.

One advantage of approaching plant-microbe interactions from a community selection perspective is that community selection does not make any assumptions about the level at which selection is occurring or whether selection acts on the holobiont as a unit [4]. In this approach, we simply define the holobiont as a community of organisms and micro-organisms in which community selection can occur [4]. Central to theories of community evolution is the concept of heritability. This aspect is often confused with inheritance, but they refer to two different processes. Inheritance is the vertical transmission of members of the microbiome from one generation to the other. Heritability measures how much of the variation in the microbiome can be attributed to host genetic variation [5] and it can be calculated for single microbial members or at a community level. As we will see later, we argue that heritability, when expanded to a community level, can provide useful insight into the evolution of the holobiont in agricultural settings.

BROAD-SENSE COMMUNITY HERITABILITY

Broad-sense community heritability (H^2_c) expands the concept of broad-sense heritability calculated for single microbial members to a community level [6]. In practice, it measures how much of the variation at a community level is explained by the host genotype. This can be achieved by condensing information on microbial composition into univariate scores using an ordination method, such as non-metric

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Abbreviations: H²C, broad-sense community heritability; IIGEs, interspecific indirect genetic effects; NMDS, non-metric multidimensional scaling.

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multidimensional scaling (NMDS), and estimating how much of the variation in the NMDS score can be attributed to the genetic variance of the host through an ANOVA.

Broad-sense community heritability is important because finding a statistically significant effect of the host genotype in influencing microbial community composition provides evidence of community selection [7]. In other words, it provides evidence of genetic covariance between host and microbiome, documenting a heritable effect on the host-associated microbiome due to plant phenotypes.

When community selection occurs, generating holobionts with differential survival, community evolution could lead to specific host-microbiome interactions spanning from mutualism to parasitism. Practically, broad-sense community heritability can be calculated through common garden experiments [7], in which for several plant genotypes and replicates of plant genotypes (clones) community data is measured (e.g. abundance of lichens, insects, micro-organisms) [8–10] and the ANOVA on the NMDS score is calculated, with the host genotype being the explanatory variable. In this approach, the value of community heritability is the R^2 of the ANOVA, and the P -value given by the factor plant genotype provides the likeliness of the null hypothesis being true.

Conceptually, broad-sense community heritability is proportional to the product of the broad-sense heritability of the host phenotypic traits (H^2_θ) (for example, root length, root architecture, and so forth) and the intensity of the host phenotypic effect at the microbial community level (also referred to as interspecific indirect genetic effects, IIGEs) (γ), relative to the total selection ($\gamma + E_n$), that is the sum of the community-level selection intensity (the effect of IIGEs) and other sources of variation in the microbiome community (E_n) (for example, soil chemical and physical properties) [7].

$$H^2_C \propto H^2_\theta \frac{\gamma}{\gamma + E_n}$$

IIGEs could be seen as equivalent to the host-to-microbe effects used in the framework of Foster *et al.* [9], however, IIGEs can be more generally applied to any community interactions. When host phenotypic effects on microbial communities (IIGEs) are weak (low γ), and the proportion of total selection due to other sources of variation is relatively high (high E_n), broad-sense community heritability approaches zero [7]. For example, low microbial broad-sense community heritability could be the result of transplanting plants into different soils, with the consequence that the soil microbiome is the main determinant of the rhizosphere microbiome [11] (the rhizosphere is the region in the vicinity of plant roots that is inhabited by a distinctive population of microorganisms which is influenced by plant roots). Under these conditions, any IIGEs resulting from certain root phenotypic traits could be overcome by stronger drivers of microbiome assembly, in this case, the different soils (high E_n), and, the rhizosphere microbiome would have low broad-sense community heritability.

EFFECT OF PLANT DOMESTICATION ON BROAD-SENSE COMMUNITY HERITABILITY

In our recent work [12] we conceptualized how the domesticated plant microbiome could differ from that of wild progenitors due to an effect of domesticated plant phenotypes by expanding the ‘ecosystem on a leash’ framework of Foster *et al.* [13]. We proposed that in domesticated plants the plant microbiome can be conceptualized as being subject to a ‘double leash’ that includes the effect of artificial selection imposed by the domesticator on plant traits and the effect of plant traits on the microbiome. We predicted a reduction in positive-microbe-to-host effects when domesticated plant phenotypes arose due to artificial selection. However, we did not discuss how our double-leash framework could be investigated at a community level. In this sense, broad-sense community heritability could help us to understand how community evolution may have been affected in domesticated vs wild plants. This is important because community evolution could lead to new community phenotypes (holobiont phenotypes) that could have important agricultural repercussions. For example, as discussed below, loss of plant heritable phenotypic variation, often associated with plant domestication, could lead to a reduction in community evolution potential, which in turn could result in plant holobionts that are less resilient to environmental stresses than their wild progenitors.

We propose that plant domestication could lower broad-sense community heritability of the host-microbiome by (1) reducing community-level selection on the microbiome (γ), and (2) increasing other potential sources of variation in the host-microbiome community (E_n).

Effect of plant domestication on community-level selection (γ)

One of the main consequences of plant domestication has been a reduction in plant genetic diversity (domestication bottleneck) [14]. Phenotypic traits in wild ancestors with potentially high IIGEs on the microbial community could have been lost due to the domestication bottleneck [15], particularly if these traits did not contribute positively to the plant phenotype from the domesticators’ point of view [12]. The effect of domesticated plant phenotypic traits on microbiome assembly, such as root length and plant height have been investigated for wheat [16] and common bean [17], showing that plant traits can have strong IIGEs. The probability of losing plant phenotypic traits with high IIGEs would increase with the strength of the domestication bottleneck (Fig. 1a), as the more genetic diversity is lost, the more likely it is that plants will lose heritable plant traits, which exert IIGEs.

Additionally, artificial selection could have directly selected against certain plant phenotypes if those traits were unsuitable for an agricultural ecosystem. For example, the reduction of plant secondary metabolites to make plants more palatable or less toxic

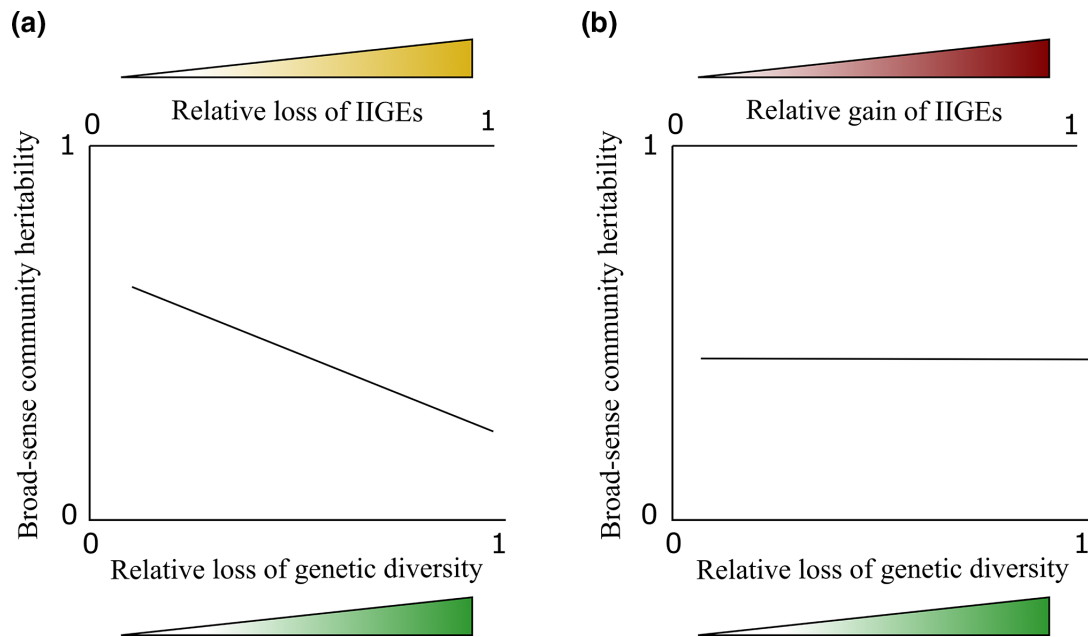


Fig. 1. Effect of plant domestication on broad-sense community heritability depends on the combined effect of the domestication bottleneck and the IIGEs of the host phenotypes. (a) A reduction in plant genetic diversity due to domestication can lead to loss of host phenotypes with strong IIGEs (e.g. concentration of secondary metabolites), which results in a reduction in community heritability of the microbiome. This could be exacerbated when traits subject to artificial selection in domesticated plant phenotypes exert low IIGEs on the microbial communities (e.g. traits selected for aesthetic purposes). (b) When domesticated plant phenotypes exert low IIGEs, loss of plant phenotypes due to the domestication bottleneck could be compensated, assuming there are sufficient heritable phenotypic variations to observe the effect of these plant phenotypes. Under these conditions, a reduction in broad-sense community heritability may not occur. Axes for loss of genetic diversity and IIGEs refer to relative loss/gain (range 0–1). The x-axis for broad-sense community heritability is also relative (range 0–1) and represents the total microbial community variation condensed into NMDS scores that can be attributed to host genotypes (see main text for details).

is a common feature of domesticated crops [18]. Secondary metabolites are known to play an important role in host–microbe interactions [19, 20], possibly exerting high IIGEs.

Thus, we might generally predict to observe a reduction in both community-level selection and in broad-sense community heritability as a consequence of domestication, which is consistent with the double-leash hypothesis. However, an essential condition for community selection to occur is the existence of heritable plant phenotypic variations exerting IIGEs. If domesticated plant phenotypes exert strong host-to-microbe effects, but there is little or no heritable plant phenotypic variation in IIGEs across individuals, community selection at holobiont level cannot occur. However, providing there is heritable phenotypic variation, broad-sense community heritability of the domesticated plant microbiome would not necessarily decrease with the strength of the domestication bottleneck as the loss of plant phenotypes could be balanced out by strong IIGEs induced by domesticated plant phenotypes (Fig. 1b).

Effect of plant domestication on other sources of variation in the microbiome community (E_n)

The effects of domestication on plant phenotypes and the plant microbiome also need to be interpreted in the context of agricultural environments, in which agricultural inputs such as fertilization or soil management practices can have a larger effect on the host-associated microbiome than IIGEs of host traits, thus increasing E_n [21]. For example, inorganic nitrogen applications have been shown to affect both taxonomical and functional profiles of rhizosphere microbial communities of wheat [22]. At the same time, intensive agriculture reduces soil microbiome alpha-diversity, creating biotic homogenisation [23]. This could ultimately limit the number of community members affected by IIGEs.

MICROBIOME BROAD-SENSE COMMUNITY HERITABILITY OF DIFFERENT PLANT COMPARTMENTS

While in some contexts it is useful to consider broad-sense community heritability at the level of the whole plant, it is also important to consider that different host compartments can be colonized by different, but interconnected microbial communities [11, 24]. Therefore, a host phenotypic trait (e.g. leaf tannin concentration) could have different IIGEs on microbial communities

inhabiting different host compartments [e.g. the phyllosphere (above ground plant surfaces that can be colonized by micro-organisms) microbiome compared to the rhizosphere microbiome]. In this example, while the phyllosphere microbiome could be affected directly by tannin concentrations in leaves, the rhizosphere microbiome could be also affected as leaves fall on the ground, where they contribute to and are decomposed by the soil microbiota. In turn, the seed microbiome could be affected by changes in the assembly of the phyllosphere and rhizosphere microbiome, which both contribute micro-organisms to the seed microbiome.

At the same time, even within the same plant compartment, microbial communities change dynamically based on the plant developmental stage [25]. For this reason, microbial communities inhabiting different plant compartments at different developmental stages will have different broad-sense community heritability. The domestication process will, therefore, differentially affect microbial broad sense community heritability depending on the host compartment, developmental stage and the interaction of host compartments. The effect of IIGEs is also likely to be stronger where community diversity is lower (e.g. endophytes vs non-endophytes) [13] (endophytes are micro-organisms living inside a plant compartment). For this reason, we would expect broad-sense community heritability to be higher for endophytic microbial communities, which can then lead to stronger community-level selection.

PRACTICAL IMPLICATIONS

Approaching the holobiont from a community evolution perspective could enable us to better understand the evolution of the holobiont and identify plant traits leading to the assembly of specific microbial communities. This view is different but complementary to what we have described in our double-leash framework, which focuses on the host individual level. The double-leash framework posits that when domesticated plant phenotypes are selected through artificial selection by the domesticator and they have no consequences for plant fitness, these traits are unlikely to have evolved as an attempt of the host to control the microbiota and receive positive microbe-to-host effects. The community evolution perspective also supports the conceptual development of scenarios in which domestication could lead to reduced community selection through a reduction in IIGEs, irrespective of whether interactions have positive implications for the host, and requires us to consider the possibility that a loss of genetic diversity could lead to scenarios where heritable variation in plant phenotypic traits exerting IIGEs is insufficient for community selection to occur.

One criticism could be that it is unlikely that important IIGEs were lost during domestication as the domesticator would have selected against ‘compromised’ holobionts. However, domesticators cannot predict future conditions that would benefit from lost IIGEs that at the time selection was exerted were not important. For example, root trait variation is reduced in domesticated plants [26]. Selection of domesticated plants with reduced root phenotypic variation compared to wild plants may not have major consequences at present. Nonetheless, environmental stresses such as drought are becoming more frequent as a result of climate change [27]. The introduction of higher variation in root phenotypes through crossing with wild progenitors could enable the evolution of holobionts more tolerant to environmental stress as a result of community (holobiont) selection, where enough root trait variation exerting IIGEs exists.

Importantly, viewing plant domestication through the lens of community evolution facilitates the design of experiments to detect and quantify IIGEs, which will not only help us to understand whether domestication has led to a loss in plant phenotypic variation that was exerting strong IIGEs, but could also enable us to identify plant traits responsible for certain aspects of microbiome assembly.

A simple initial experiment could be to grow wild and domesticated plants in a small geographical area in their correspondent ecosystems, that is natural ecosystems for wild plants (or as close as possible to natural) and agricultural for domesticated plants. Plant genotypes should be selected to encompass the population genetic diversity of the species being studied (Fig. 2a). Each genotype would be replicated paying attention that replicates of the same genotype are identical (clones or highly homozygous individuals). The microbiome of different plant compartments would then be sampled and analysed for both wild and domesticated plant populations. This simple experiment could help us understand (i) how wild and domesticated plants differ in terms of community selection by plant compartment, (ii) whether domesticated plants have lower broad-sense community heritability compared to wild progenitors. This would help demonstrate whether domestication has led to (i) a reduction in IIGEs, (ii) insufficient heritable plant phenotypic variation to detect IIGEs, or (iii) a combination of both.

Moreover, these results could lead to the identification of plant compartments for which a reduction of broad-sense community heritability has occurred in domesticated plants compared to wild types. In the hypothetical example shown in Fig. 2a, broad-sense community heritability of the root compartment in wild-type is higher than in domesticated plants. In this scenario, subsequent experiments involving progeny from crosses and backcrosses between wild and domesticated plants and genome-wide association studies would help to identify which plant genotypes and phenotypes are exerting IIGEs (Fig. 2b). An alternative approach would be to examine correlations between plant traits and microbiome assembly, as reported in common bean for root length [17].

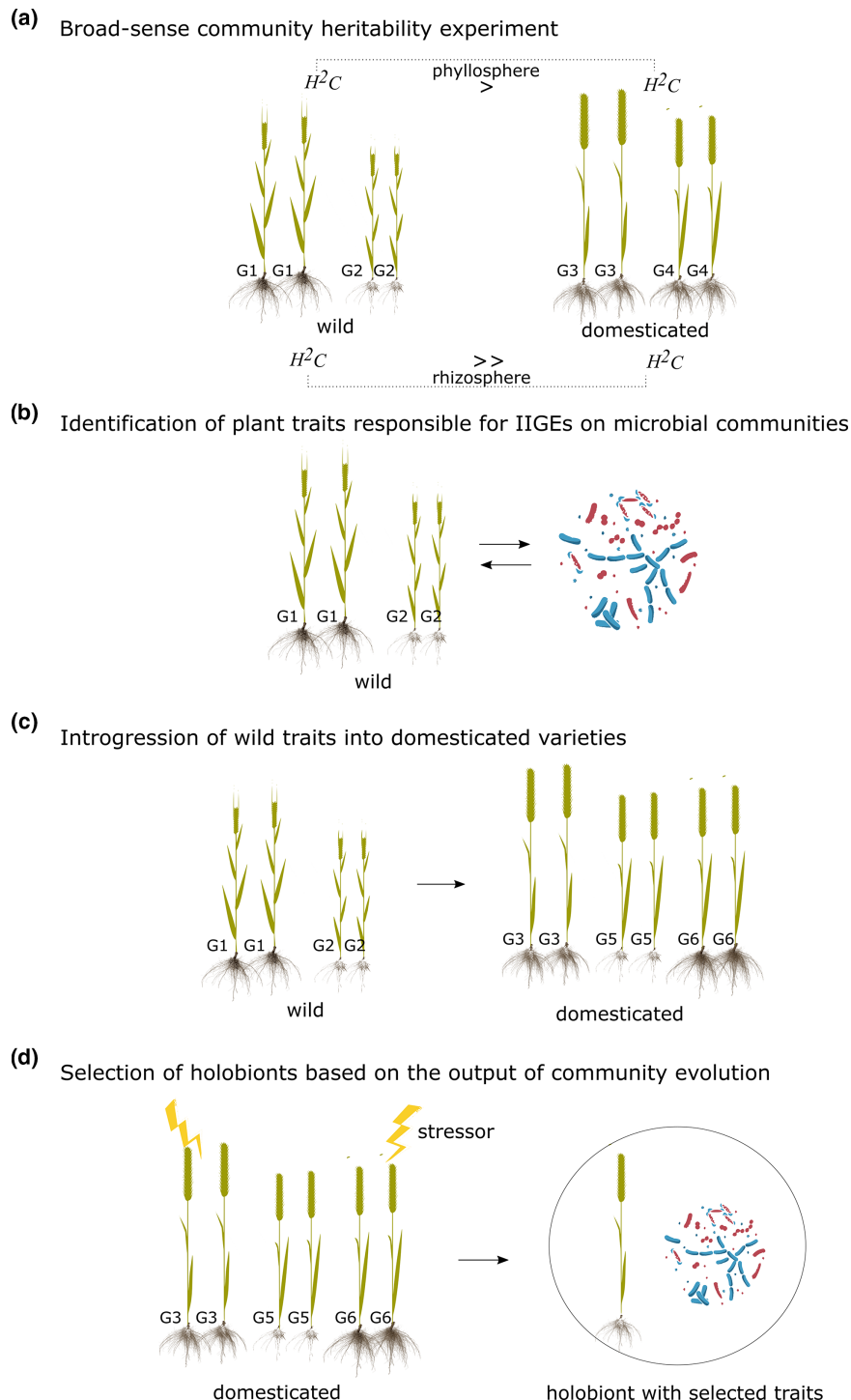


Fig. 2. An experimental framework to enhance community evolution potential in domesticated crops. (a) Analysis of whether broad-sense community heritability is reduced in domesticated plants. Wild and domesticated plants are grown in their correspondent ecosystems [natural ecosystem for wild plants (or as close as possible to natural) and agricultural for domesticated plants]. Plant genotypes (G_n) should be selected to encompass the population genetic diversity of the species being studied. Replicates of the same genotype should be clones or highly homozygotic individuals. Broad-sense community heritability of different plant compartments is then assessed. In the example shown, both the phyllosphere and rhizosphere compartments of domesticated plants have lower broad-sense community heritability than wild progenitors, but the difference in broad-sense community heritability between wild and domesticated plants is more pronounced for the rhizosphere ($>>$). (b) Backcrossing, GWAS, and multivariate statistics aimed at linking plant traits to microbiome assembly can help to identify plant genotypes and phenotypes exerting IIGEs. (c) Traits responsible for IIGEs are reintroduced into domesticated plants, reestablishing heritable phenotypic variation leading to community selection. (d) Once genetic variation associated with IIGEs is reintroduced into domesticated crops, community evolution can lead to the emergence of new holobionts with new environmental potentials. For example, selection schemes could include the application of stresses, such as drought, and select the holobionts with higher potential in terms of yield, drought resistance, or any other trait of interest.

Having found evidence of loss of IIGEs, introgression of wild germplasm into domesticated populations could reintroduce variation in IIGEs and reprimatinate the potential for community evolution in domesticated plants to occur (Fig. 2c). Subsequently, experiments aimed at selecting the best performing holobionts in certain environmental conditions, such as drought, could be performed (Fig. 2d). The feature for selection could be crop yield or any other trait of interest. The proposed approach would facilitate selection at the holobiont level by first addressing whether domestication has reduced community selection potential.

CONCLUDING REMARKS

Approaching the holobiont, defined as host and host-associated microbiome, from a community level perspective avoids many of the debated aspects of holobiont theories, such as co-evolution and inheritance. In the context of plant domestication, approaching the holobiont from a community-level prospect could give us a more holistic view of plant–microbe interactions in the agricultural ecosystem, pave the way to the identification of plant traits exerting strong IIGEs and cast light on the assembly of domesticated plant microbiomes.

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Author contributions

R.S. conceived the idea; R.S. and G.M.P. wrote the manuscript with inputs from MF. All authors critically revised the manuscript.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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