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Focused Identification of Germplasm Strategy (FIGS): polishing a rough diamond

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Focused Identification of Germplasm Strategy (FIGS) has been advocated as an efficient approach to predict and harness variation in adaptive traits in genebanks or wild populations of plants. However, a weakness of the current FIGS approach is that it only utilizes *a priori* knowledge of one evolutionary factor: natural selection. Further optimization is needed to capture elusive traits, and this review shows that nonadaptive evolutionary processes (gene flow and genetic drift) should be incorporated to increase precision. Focusing on plant resistance to insect herbivores, we also note that historic selection pressures can be difficult to disentangle, and provide suggestions for successful mining based on eco-evolutionary theory. We conclude that with such refinement FIGS has high potential for enhancing breeding efforts and hence sustainable plant production.

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Introduction

Pests and pathogens pose major threats to domesticated crops [1] and optimal strategies are needed to minimize damage. Intrinsic plant resistance should play a fundamental role in these strategies, especially since Integrated Pest Management (IPM) has been globally embraced as the future paradigm for plant protection [2]. Unfortunately, the strong contemporary demand for resistant cultivars cannot be easily met, as important resistance traits have been lost during domestication [3,4]. Thus, landraces and wild relatives of crops that still harbor important resistance traits must often be revisited to meet needs for resistance [5•,6]. This is because continuous natural selection (including by herbivores) prevents the loss of adaptive traits in their wild or cultivated environments. Thus, restoring lost resistance traits (known as ‘rewilding’) in modern cultivars using these wild genetic resources is a major goal for IPM [7•].

Unfortunately, mining for rare genetic resources in wild populations and genebanks is often extremely difficult and time consuming, due to the enormous amounts of material available for screening *ex situ* and *in situ*. Searching for material with specific rare traits is thus frequently likened to looking for a needle in a haystack [8]. Core or representative subsets of germplasm collections [9] can be established to reduce search efforts. However, their creation and classification are not typically based on specific resistance traits, so this approach (in current formats) does not help breeders to focus on the most promising material. However, *Focused Identification of Germplasm Strategy* (FIGS) provides a new way to maximize the likelihood of capturing plant genotypes with specific adaptive traits from genebanks and wild populations [10]. The rationale is that certain types of environments mediate natural selection, for or against, the adaptive evolution of focal plant traits in wild populations and cultivated landraces. Hence, the spatial distribution of adaptive plant traits should be predictable from ecogeographic profiles of plant trait distributions, allowing trait miners to focus on limited numbers of georeferenced germplasm samples, originating solely from evolutionary ‘hotspots’. Thus, the ‘focus’ in FIGS may refer to both the specific adaptive trait(s) of interest and specific environmental profiles corresponding to evolutionary hotspots.

In the last decade, the FIGS approach has been used to harness various traits, including *inter alia* drought tolerance [11], plant size and flower number [12•], as well as resistance to pathogens [13–15], and herbivores [16–18]. However, as noted by various authors [10,12•,15], FIGS is still a nascent approach, with scope for significant improvement. The main weakness of current FIGS is that it only utilizes *a priori* knowledge about one evolutionary factor: natural selection. This limits its potential utility because focal traits may not have been strongly influenced by natural selection and/or historic selection pressures (exerted by herbivores for example) may be difficult to determine. Thus, associations between focal traits and ecogeographic data may be weaker than expected [19]. Further challenges are associated with insect resistance, as the underlying traits must be identified. Here we discuss these challenges in the light of recent literature and suggest possible ways to improve FIGS, particularly in relation to insect resistance.

Challenges and opportunities related to resistance traits

Plants can be resistant to insects in myriad ways, involving *inter alia* trichomes, leaf toughness, toxic compounds, kairomones, or extrafloral nectar [20,21]. While highly specialized plant–insect interactions may depend on single plant traits, most herbivores – especially chewing species – are sensitive to several types of resistance traits [22], which may be shaped by multiple selection pressures. Thus, individual plants within their species' range may allocate different amounts of resources to specific resistance traits, just as the overall resistance level typically varies [18,23••].

As FIGS focuses on individual traits, the first step in a FIGS process is to identify all known or likely types of resistance traits in a plant species, then select the most optimal trait according to several criteria. First, the selected resistance trait should clearly reduce herbivore damage as efficiently as possible [24]. Second, it should be compatible with IPM, and thus not hamper biocontrol agents or other beneficial organisms [2,25]. Third, it should be acceptable to human consumers, as consumer rejection is a major reason for the selection against, and loss of, some resistance traits during domestication [26•]. Such undesirable traits include, among others, bitterness, toughness, and some characteristics related to unacceptable metabolic costs that may incur yield penalties. 'Rewilding' will not necessarily reintroduce these 'problematic' traits, as wild relatives of crops and landraces often have a rich palette of resistance traits from which breeders can select. Finally, to be compatible with FIGS the selected trait should, of course, be prone to adaptation under directional selection.

Identifying specific resistance traits that are particularly compatible with FIGS is beyond the scope of this review, but generally we believe that modern crossbreeding should focus more on indirect resistance, that is, traits that recruit natural enemies of herbivores [27]. Traits underlying indirect resistance are typically induced, rarely require substantial resources from the plant's metabolic budget [28] and are available in landraces and wild relatives of most crops [29,30]. Moreover, they are adaptive [31,32] and the underlying genes are increasingly being identified, for example, through genome-wide association studies [32].

Predicting historic selection

Generally, biotic selection is a key driver of plants' evolution [33] and can rapidly shape and reshape their resistance traits [34,35]. Hence, plant traits related to insect resistance are among those with the clearest potential for FIGS. However, although some or most resistance traits are under selection by herbivores, the same traits may also respond to other, conflicting selective pressures, potentially leading to low correlation between historic selection by herbivores and resistance [36]. For example, resistance compounds in floral nectar may deter pollinators, leading to conflicting selection by herbivores and pollinators, and thus 'diffuse' plant evolution [37••,38]. The outcome of such diffuse selection may depend on the relative importance of the players involved, as well as the extent of their spatial overlap, which may lead to spatially divergent plant populations. In other cases, some traits may have multiple positive roles. For example, a trait may confer resistance to both herbivory and abiotic stress, like frost or drought [39,40•]. In such cases, abiotic selection pressures on resistance traits may lead to strong insect resistance even in areas where herbivory is low [41]. Thus, knowledge of the multifunctionality of resistance traits is crucial for robust predictions of historic selection pressures for use in FIGS.

Nevertheless, although other biotic and abiotic factors are important, in most cases the historic distribution of keystone herbivores is the most important factor for predicting distributions of historic selection pressures on resistance traits [42]. Generally, climatic clines (e.g. latitude and altitude) and resource availability have received the most attention for their roles in shaping herbivore distributions, and evolution of plant resistance [23••,43,44]. Latitude and altitude correlate negatively with temperature and length of the growing season, and thus are relatively good proxies for herbivore diversity and herbivore pressure, although no such relationships (or even opposite patterns) have been observed in analyses of several plant species' environmental interactions [45].

Early reporters of significant associations between host plant resistance to insects and ecoclimatic profiles of the collection sites of accessions in genebanks included Flanders *et al.* [46]. They found that accessions of *Solanum* from hot and arid zones showed resistance to Colorado potato beetle, potato flea beetle and potato leafhopper, while species from cool or moist areas showed resistance to potato aphid. In further research involving use of data pertaining to 92 *Solanum* species obtained from two decades of field trials, the same group [47] demonstrated that insect resistance of the genus was not evenly distributed in the American continent, but varied with the altitude and in some cases latitude of their origins.

Although many plant species show higher overall resistance in areas at low latitudes or altitudes, this does not necessarily mean that these areas are always hotspots for valuable resistance traits in FIGS. As single resistance traits rather than overall resistance levels are ideally used in FIGS, focal individual traits may respond more strongly in low-diversity communities, where specific herbivores contribute more strongly to the direction of net selection. There is, in any case, no doubt that climatic and resource clines should be utilized in FIGS, but the direction of the putative correlations should ideally be roughly confirmed by pre-studies. Clines shaping plant traits can be very narrow, so small-scale patterns warrant attention as well as larger scale patterns [12•]. Other natural factors affecting herbivore distributions, such as precipitation, winter temperature and habitat have also been successfully integrated into FIGS [10, Stenberg, unpublished data], but are not further considered here due to space limitation.

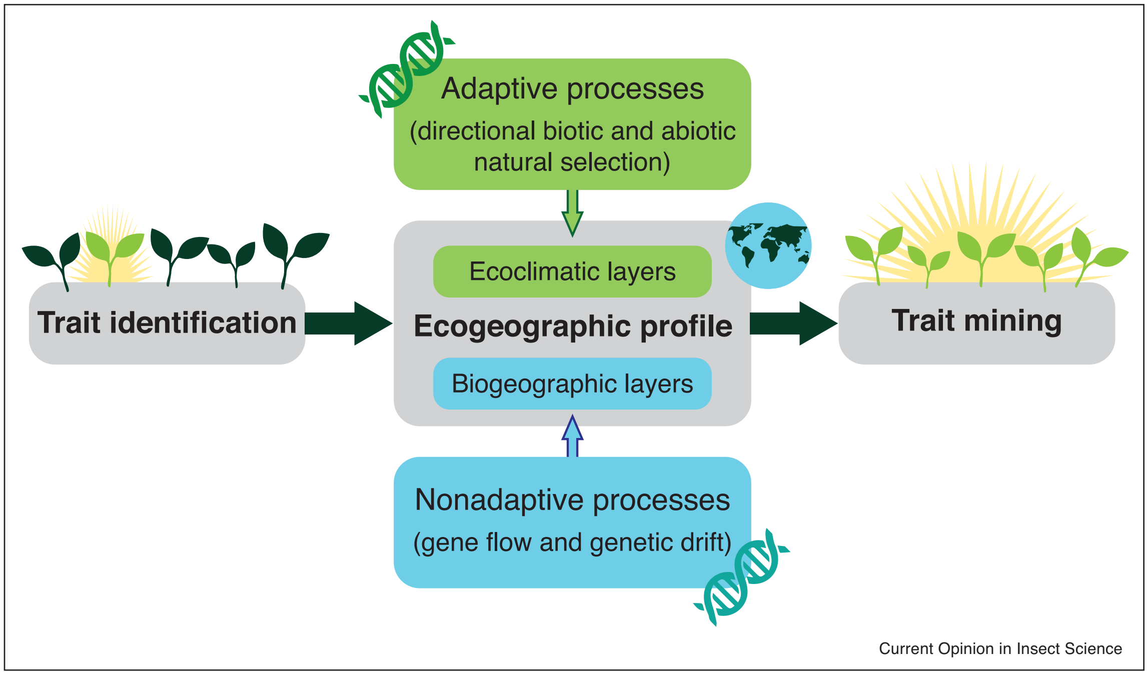
In addition to identifying hotspots based on natural environmental factors, as discussed above, awareness is needed that human activities repeatedly expanded distributions of crop wild relatives. Thus, they escaped from some of their old herbivores, leading to loss or remolding of resistance in their new areas [48]. For these reasons, identifying native areas where both the plants and herbivores have interacted historically, and filtering out more novel distributions, has been a key step in practical application of FIGS [10].

In practical terms, proxies of historic natural selection have been implemented as *ecoclimatic layers* to form *ecogeographic profiles* for focal traits in FIGS (Figure 1). Although these search profiles have helped efforts to harness important traits for several plants, many authors have also noted lower than expected correlations between ecoclimatic data and focal traits, highlighting the need to develop FIGS [10,12•,15]. However, as shown below, evolutionary hotspots can be more precisely identified if *biogeographic layers* of nonadaptive proxies are added to the *ecogeographic profiles*.

Incorporating nonadaptive evolutionary processes into FIGS

The best way in our view to improve FIGS' precision is to consider nonadaptive evolutionary factors in parallel with directional natural selection. The importance of gene flow and genetic drift in the evolution of resistance and other traits of wild plants has been demonstrated in several recent studies [49•,50••]. Our understanding of how selection, gene flow and genetic drift jointly shape the geographic distribution of traits has increased tremendously in recent years following developments in metapopulation ecology and the geographic mosaic of coevolution theory [51,52]. A key assumption in these frameworks is that species' distributions are patchy, consisting of local plant populations that are connected to varying degrees within larger metapopulations [51,52]. Some local populations may be colonized by certain keystone herbivores, which impose selection pressure for specific traits. Other populations may host other herbivores selecting for other traits, and another set of local populations may inhabit an enemy-free environment that promotes loss of resistance

Figure 1



Conceptual framework for *Focused Identification of Germplasm Strategy* (FIGS). The first step in the FIGS process is to identify the type of trait that would be most ideal to confer a desired outcome (e.g. reduction in damage pests cause to a particular plant). Then information about the adaptive and nonadaptive evolutionary processes shaping this trait and its geographic distribution should be obtained and applied in the form of ecoclimatic and biogeographic layers in an ecogeographic profile that highlights the most intense evolutionary hotspots in the plant's range. Focusing trait mining efforts on germplasm from these hotspots should be considerably more fruitful than focusing on other areas.

[42]. Local herbivore populations in turn can go extinct or recolonize populations, molding and remolding natural plants over time and space, creating geographic mosaics with predictable evolutionary hotspots. The more isolated a local population is, the more it will be affected by local selection and small populations may also be characterized by strong genetic drift. By contrast, more connected populations will be affected not only by local selection, but also by higher gene flow that dilutes local selection through inflows of phenotypes that are evolutionary products of neighboring populations with different selection regimes [52]. Asymmetric gene flow (e.g. higher immigration than emigration, leading to dilution of local selection) is expected for small populations neighboring big ones and for low-altitude populations exposed to genetic 'rainfall' from higher-altitude populations [50••].

Obtaining knowledge about gene flow and drift may necessitate zooming in and utilizing biogeographic data at more local geographic scales. In practical terms, data on landscape (habitat) isolation and geographic distances between populations can be used as proxies of gene flow [11]. Genetic drift is partly dependent on gene flow, but relatively independent proxies include population size and recent colonization ('founder effects'). Together, data on these nonadaptive proxies can be described as *biogeographic layers*, which can be applied in e*cogeographic profiles* for focal traits in FIGS (Figure 1).

Concluding remarks

All plant traits and their distributions are products of evolution, but the relatively few published attempts to apply FIGS in practice, to enhance crop plants' insect resistance for instance, suggest that partial knowledge of natural selection does not always provide sufficient precision to capture elusive traits. To improve FIGS it is important to catch up with corresponding progress in basic eco-evolutionary theory. First, to improve prediction of adaptive processes it is necessary to identify conflicting or concurrent selection pressures imposed by other agents and integrate them into the ecogeographic profile (Figure 1). Second, following previous suggestions [11], biogeographic proxies of nonadaptive processes (gene flow and genetic drift) should ideally be routinely considered in future FIGS dealing with elusive traits (Figure 1). These adjustments to FIGS should help breeders to identify the most promising evolutionary hotspots for trait mining.

Furthermore, resistant genebank accessions identified via FIGS can be used for genomic prediction based on characterization with genotyping by sequencing as training populations. This may lead to identification of useful diversity hotspots hosting genotypes that can be advantageously used introgressively in breeding programs. This approach was proposed to improve grain yield in wheat [53], and subsequently shown to have promising potential to raise biomass yields of sorghum [54]. Such 'turbo-charging' of genebanks offers a cost-effective strategy to tap their valuable plant genetic resources by shifting from 'gene mining' to estimating accessions' breeding values through genomics.

Conflict of interest statement

Nothing declared.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- • of special interest
- •• of outstanding interest

1. Oerke E: **Crop losses to pests**. *J Agric Sci* 2006, **144**:31-43.

2. Stenberg JA: **A conceptual framework for integrated pest management**. *Trends Plant Sci* 2017, **22**:759-769.

3. Coll-Aráoz MV, Hill JG, Luft-Albarracin E, Virla EG, Fernandez PC: **Modern maize hybrids have lost volatile bottom-up and top-down control of *Dalbulus maidis*, a specialist herbivore**. *J Chem Ecol* 2020, **46**:906-915.

4. Solís-Montero V, Martínez-Natarén DA, Parra-Tabla V, Ibarra-Cerdeña C, Munguía-Rosas MA: **Herbivory and anti-herbivore defences in wild and cultivated *Cnidoscolus aconitifolius*: disentangling domestication and environmental effects**. *AoB PLANTS* 2020, **12**:plaa023.

5. • Amanuel T, Paliwal R, Manthi SJ, Odeny DA, Midega CAO, Khan ZR, Pickett JA, Bruce TJA: **Genome wide association analysis of a stemborer egg induced "call-for-help" defence trait in maize**. *Sci Rep* 2020, **10**:11205.

This research group has previously shown that landraces of maize retain important indirect resistance traits, incl. herbivore-induced plant volatiles that attract natural enemies of herbivores. Here, the authors carried out GWAS to identify genomic regions associated with indirect defence. Together with other recent papers from this group, these results show that indirect resistance traits are of key interest for rewilding of staple crops.

6. Maxted N, Hunter D, Ortiz Ríos R: *Plant Genetic Conservation*. Cambridge, UK: Cambridge University Press; 2020.

7. • Karlsson Green K, Stenberg JA, Lankinen Å: **Making sense of Integrated Pest Management (IPM) in the light of evolution**. *Evol Appl* 2020, **13**:1791-1805.

Integrated Pest Management (IPM) is the future global paradigm for plant protection and this paper puts it in an evolutionary perspective, showing how crop wild relatives can contribute to more sustainable (environmentally and evolutionary) strategies together with other IPM actions.

8. Wambugu PW, Ndjiondjop M-N, Henry RJ: **Role of genomics in promoting the utilization of plant genetic resources in genebanks**. *Brief Funct Genomics* 2018, **17**:198-206.

9. Frankel OH: **Genetic perspectives of germplasm conservation**. In *Genetic Manipulation: Impact on Man and Society.* Edited by Arber WK, Llinensee K, Peacock WJ, Starlinger P. Cambridge University Press; 1984:161-170.

10. Street K, Bari A, Mackay M, Amri A: **How the Focused Identification of Germplasm Strategy (FIGS) is used to mine plant genetic resources collections for adaptive traits**. In *Enhancing Crop Genepool Use: Capturing Wild Relative and Landrace Diversity for Crop Improvement.* Edited by Maxted N, Dulloo ME, Ford-Lloyd BV. CABI; 2016:54-63.

11. Khazaei H, Street H, Bari A, Mackay M, Stoddard FL: **The FIGS (Focused Identification of Germplasm Strategy) approach identifies traits related to drought adaptation in *Vicia faba* genetic resources**. *PLoS One* 2013, **8**:e63107.

12. • Egan PA, Muola A, Stenberg JA: **Capturing genetic variation in crop wild relatives: an evolutionary approach**. *Evol Appl* 2018, **11**:1293-1304.

This paper represents the first, and so far only, attempt to integrate nonadaptive processes into FIGS. The results show that gene flow is an important evolutionary factor shaping wild strawberry traits, suggesting that proxies of nonadaptive processes routinely should be considered in future FIGS attempts.

13. Endresen DTF, Street K, Mackay M, Bari A, De Pauw E: **Predictive association between biotic stress traits and eco-geographic data for wheat and barley landraces**. *Crop Sci* 2011, **51**:2036-2055.

14. Endresen DTF, Street K, Mackay M, Bari A, Amri A, De Pauw E, Nazari K, Yahyaoui A: **Sources of resistance to stem rust (Ug99) in bread wheat and durum wheat identified using Focused Identification of Germplasm Strategy**. *Crop Sci* 2012, **52**:764-773.

15. Bari A, Street K, Mackay M, Endresen DTF, De Pauw E, Amri A: **Focused Identification of Germplasm Strategy (FIGS) detects wheat stem rust resistance linked to environmental variables**. *Genet Resour Crop Evol* 2012, **59**:1465-1481.

16. El Bouhssini M, Street K, Joubi A, Ibrahim Z, Rihawi F: **Sources of wheat resistance to Sunn pest, *Eurygaster integriceps* Puton, in Syria**. *Genet Resour Crop Evol* 2009, **56**:1065-1069.

17. El Bouhssini M, Street K, Amri A, Mackay M, Ogbonnaya FC, Omran A, Abdalla O, Baum M, Dabbous A, Rihawi F: **Sources of resistance in bread wheat to Russian wheat aphid (*Diuraphis noxia*) in Syria identified using the Focused Identification of Germplasm Strategy (FIGS)**. *Plant Breed* 2011, **130**:96-97.

18. Weber D, Egan PA, Muola A, Stenberg JA: **Genetic variation in herbivore resistance within a strawberry crop wild relative (*Fragaria vesca* L.)**. *Arthropod Plant Interact* 2020, **14**:31-40.

19. Jansky SH, Simon R, Spooner DM: **A test of taxonomic predictivity: resistance to the Colorado potato beetle in wild relatives of cultivated potato**. *J Econ Entomol* 2009, **102**:422-431.

20. Aljbory Z, Chen M-S: **Indirect plant defense against insect herbivores: a review**. *Insect Sci* 2018, **25**:2-23.

21. Volf M: **Differential response of herbivores to plant defence**. In *Co-evolution of Secondary Metabolites.* Edited by Mérillon J-M, Ramawat KG. Springer; 2020:77-100.

22. Pearse IS, Paul R, Ode PJ: **Variation in plant defense suppresses herbivore performance**. *Curr Biol* 2018, **28**:1981-1986.

23. •• Hahn PG, Agrawal AA, Sussman KI, Maron JL: **Population variation, environmental gradients, and the evolutionary ecology of plant defense against herbivory**. *Am Nat* 2019, **193**:20-34.

One of few studies that screened the geographic variation of several different resistance traits simultaneously. Several traits correlated with climatic clines, and climatically favorable areas seemed to facilitate the evolution of greater resistance.

24. Stenberg JA, Muola A: **How should plant resistance to *herbivores* be measured?** *Front Plant Sci* 2017, **8**:663.

25. Egan PA, Dicks LV, Hokkanen HMT, Stenberg JA: **Delivering integrated pest and pollinator management**. *Trends Plant Sci* 2020, **25**:577-589.

26. • Moreira X, Abdala-Roberts L, Gols R, Francisco M: **Plant domestication decreases both constitutive and induced chemical defences by direct selection against defensive traits**. *Sci Rep* 2018, **8**:12678.

These authors compared constitutive and induced resistance traits in wild cabbage with domesticated varieties and found that domestication had reduced the levels of both these types of traits. They further concluded that loss of resistance in domesticated cabbage is the result of direct selection rather than indirect effects via trade-offs.

27. Stenberg JA, Heil M, Åhman I, Björkman C: **Optimizing crops for biocontrol of pests and disease**. *Trends Plant Sci* 2015, **20**:698-712.

28. Hoballah ME, Köllner TG, Degenhardt J, Turlings TCJ: **Costs of induced volatile production in maize**. *Oikos* 2004, **105**:168-180.

29. Chen YH, Gols R, Benrey B: **Crop domestication and its impact on naturally selected trophic interactions**. *Annu Rev Entomol* 2015, **60**:35-58.

30. Weber D, Egan PA, Muola A, Ericson LE, Stenberg JA: **Plant resistance does not compromise parasitoid-based biocontrol of a strawberry pest**. *Sci Rep* 2020, **10**:5899.

31. Rutter MT, Rausher MD: **Natural selection on extrafloral nectar production in *Chamaecrista fasciculata*: the costs and benefits of a mutualism trait**. *Evolution* 2007, **58**:2657-2668.

32. De Lange ES, Farnier K, Degen T, Gaudillat B, Aguilar-Romero R, Bahena-Juárez F, Oyama K, Turlings TCJ: **Parasitic wasps can reduce mortality of teosinte plants infested with fall armyworm: support for a defensive function of herbivore-induced plant volatiles**. *Front Ecol Evol* 2018, **6**:55.

33. Hembry DH, Weber MG: **Ecological interactions and macroevolution: a new field with old roots**. *Annu Rev Ecol Evol Syst* 2020, **51**:215-243.

34. Jack CN, Friesen ML: **Rapid evolution of *Medicago polymorpha* during invasion shifts interactions with the soybean looper**. *Ecol Evol* 2019, **9**:10522-10533.

35. De-la-Cruz IM, Cruz LL, Martínez-García L, Valverde PL, Flores-Ortiz CM, Hernández-Portilla LB, Núñez-Farfán J: **Evolutionary response to herbivory: population differentiation in microsatellite loci, tropane alkaloids and leaf trichome density in *Datura stramonium***. *Arthropod Plant Interact* 2020, **14**:21-30.

36. Damián X, Ochoa-López S, Gaxiola A, Fornoni J, Domínguez CA, Boege K: **Natural selection acting on integrated phenotypes: covariance among functional leaf traits increases plant fitness**. *New Phytol* 2020, **225**:546-557.

37. •• Ramos SE, Schiestl FP: **Rapid plant evolution driven by the interaction of pollination and herbivory**. *Science* 2019, **364**:193-196.

Very elegant study showing that the evolution of wild cabbage can be extremely rapid and is driven by diffuse selection involving both herbivores and pollinators, where the latter selects against chemical resistance traits. The results show that other biotic agents of selection than herbivores should ideally be considered in FIGS.

38. Sletvold N: **The context dependence of pollinator-mediated selection in natural populations**. *Int J Plant Sci* 2019, **180**:934-943.

39. Sletvold N, Ågren J: **Variation in tolerance to drought among Scandinavian populations of *Arabidopsis lyrata***. *Evol Ecol* 2012, **26**:559-577.

40. • Sack L, Buckley TN: **Trait multi-functionality in plant stress response**. *Integr Comp Biol* 2020, **60**:98-112.

These authors demonstrate, using trichomes as model trait, how single traits can have multiple functions. Understanding the various functions of resistance traits will greatly help identifying agents of selection, and thus historic selection on traits.

41. Moreira X, Castagneyrol B, Abdala-Roberts L, Berny-Mier y Teran JC, Timmermans BGH, Bruun HH, Covelo F, Glauser G, Rasmann S, Tack AJM: **Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory**. *Ecography* 2018, **41**:1124-1134.

42. Poelman EH, Kessler E: **Keystone herbivores and the evolution of plant defenses**. *Trends Plant Sci* 2016, **21**:477-485.

43. Coley PD, Aide TM: **Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests**. In *Plant-animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions.* Edited by Price PW, Lewinsohn TM, Fernandes GW, Benson WW. John Wiley & Sons; 1991:25-49.

44. Galmán A, Abdala-Roberts L, Covelo F, Rasmann S, Moreira X: **Parallel increases in insect herbivory and defenses with increasing elevation for both saplings and adult trees of oak (*Quercus*) species**. *Am J Bot* 2019, **106**:1558-1565.

45. Xiao L, Hervé MR, Carillo J, Ding J, Huang W: **Latitudinal trends in growth, reproduction and defense of an invasive plant**. *Biol Invasions* 2019, **21**:189-201.

46. Flanders K, Hawkes JG, Radcliffe EB, Lauer FI: **Insect resistance in potatoes: sources, evolutionary relationships, morphological and chemical defenses, and eco-geographical associations**. *Euphytica* 1992, **61**:83-111.

47. Flanders K, Radcliffe EB, Hawkes JG: **Geographic distribution of insect resistance in potatoes**. *Euphytica* 1997, **93**:201-221.

48. Zangerl AR, Berenbaum MR: **Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore**. *Proc Natl Acad Sci U S A* 2005, **102**:15529-15532.

49. • Johnson MTJ, Prashad CM, Lavoignat M, Saini HS: **Contrasting the effects of natural selection, genetic drift and gene flow on urban evolution in white clover (*Trifolium repens*)**. *Proc Roy Soc B* 2018, **285** 20181019.

This study elegantly examined the relative roles of adaptive and nonadaptive processes on the evolution of white clover in urban environments. It represents a growing body of literature demonstrating the importance of nonadaptive processes for plant evolution, strongly suggesting that they should be incorporated into FIGS.

50. •• Hämälä T, Savolainen O: **Genomic patterns of local adaptation under gene flow in *Arabidopsis lyrata***. *Mol Biol Evol* 2019, **36**:2557-2571.

Landscape genomics has greatly helped our understanding of the processes shaping plant evolution. This study shows that both natural selection, gene flow, and genetic drift have contributed to the evolution of *Arabidopsis* over small geographic scales. Interestingly, the results demonstrate the importance of altitude in shaping asymmetric gene flow between high and low plant populations.

51. Fernandes LD, Lemos-Costa P, Guimarães Jr PR, Thompson JN, de Aguiar MAM: **Coevolution creates complex mosaics across large landscapes**. *Am Nat* 2019, **194**:217-229.

52. Masier S, Bonte D: **Spatial connectedness imposes local- and metapopulation-level selection on life history through feedbacks on demography**. *Ecol Lett* 2020, **23**:242-253.

53. Longin CF, Reif JC: **Redesigning the exploitation of wheat genetic resources**. *Trends Plant Sci* 2014, **19**:631-636.

54. Yu X, Li X, Guo T, Zhu C, Wu Y, Mitchell SE, Roozeboom KL, Wang D, Li Wang M, Pederson GA *et al.*: **Genomic prediction contributing to a promising global strategy to turbocharge genebanks**. *Nat Plants* 2016, **2**:16150.