Evolutionary Genetics of Crop-Wild Complexes

Andrés J. Cortés 1,2,*, Amandine Cornille 3 and Roxana Yockteng 4,5

1 Corporación Colombiana de Investigación Agropecuaria AGROSAVIA, C.I. La Selva, Km 7 vía Rionegro—Las Palmas, Rionegro 054048, Colombia
2 Facultad de Ciencias Agrarias—Departamento de Ciencias Forestales, Universidad Nacional de Colombia—Sede Medellín, Medellín 050034, Colombia
3 Université Paris-Saclay, INRAE, CNRS, AgroParisTech, GQ—Le Moulon, Gif-sur-Yvette, France; amandine.cornille@cnrs.fr or amandine.cornille@inrae.fr
4 Corporación Colombiana de Investigación Agropecuaria AGROSAVIA, C.I. Tibaitatá, Km 14 vía Mosquera, Cundinamarca 250047, Colombia; ryockteng@agrosavia.co
5 Institut de Systématique, Evolution, Biodiversité-UMR-CNRS 7205, National Museum of Natural History, 75005 Paris, France
* Correspondence: acortes@agrosavia.co

Since Darwin’s time, the role of crop wild relatives (CWR), landraces, and cultivated gene pools in shaping plant diversity and boosting food resources has been a major question [1]. After all, domestication is by far the biggest evolutionary [2] and selection trial [3] carried out by humanity. Thanks to this, we have been able to test explicit hypotheses on the patterns [4] and drivers [5] of crop domestication and diversification [6–8]. Despite crop wild complexes being undeniably insightful as study systems [9], and modern developments speeding up their utilization [10], studies at the crop–wild interface remain challenging. Research requires to be conducted on natural decoupling between CWR and the cultivated gene pools in terms of their growing cycles, phenological phases, and dispersion strategies, not to mention the complexity derived from recurrent [11] crop–wild introgression patterns [12]. These difficulties have precluded reaching a trans-disciplinary synthesis on crop–wild systems.

Therefore, the goal of this Special Issue was to summarize fundamental and applied approaches on the evolutionary genetics in crop species and their CWR. Specifically, this compilation offers new insights into: (1) the evolutionary genetics of CWR [13] and the genomic consequences of domestication [14], (2) the role of crop–wild gene flow in adaptation [15], the utility to breed wild resources for climate change [16], and the necessity to consolidate open-source scientific networks [17] targeting underutilized/understudied plant resources.

1. From Early Domestication to Modern Breeding

In an effort to unveil the domestication of an ancient grain (Figure 1), Thapa et al. [13] studied the relationship of cultivated grain amaranth species and their wild relatives across a diverse panel of 276 accessions using Kompetitive Allele Specific PCR (KASP)-based single nucleotide polymorphism (SNP) markers. The authors interpreted potential domestication events. The two Mesoamerican species *Amaranthus cruentus* and *A. hypochondriacus* were inter-crossed and distantly related to the South American species *A. caudatus* and the weedy relative *A. quitensis*, both persisted in a wild-cultivated hybrid state. Future studies must validate these scenarios using demographic inferences.
Figure 1. Trans-disciplinary synthesis on crop wild complexes envisioned as part of this Special Issue. Transversal ‘big data’ tools (Ψ) [16], and consolidated research networks [17], promise promoting research integration around crop wild systems across the multi-dimensional space shaped by fundamental questions (e.g., nature and timing of domestication events, X-axis), and more applied research (e.g., underutilized/understudied crops with potential nutritional and bio-economical value, Y-axis). Specifically, genomic prediction (GP) [18], genomic-assisted back-crossing (GABC), and machine learning (ML) tools [16], boosted by open-access research networks (OA-RN) [17], would allow cohesive learning from early domestication (e.g., amaranth species [13]), and modern breeding (e.g., field cress, L. campestre [14]). Additionally, ‘big data’ and OA-RN will enable to unlock more efficiently variation hidden at crop wild complexes with nutritional value (e.g., Phaseolus bean species [15]), and those with a more industrial perspective (e.g., field cress, a promising oil crop for the subarctic [14]). Based on this compilation, we encourage oncoming studies to: (1) explicitly test evolutionary scenarios concerning the domestication of the ancient grain amaranth via approximate Bayesian computation (ABC) demographic inferences [13] and ML [19,20], (2) narrow the genetic mapping of key domestication-related traits in the modern breeding of field cress [14] via genome-wide association studies (GWAS) and GP [18], and (3) utilize tepary bean as a source of adapted alleles for drought tolerance (and potentially heat tolerance) in common bean [15] via inter-specific crossing schemes [21] and more modern GABC-based indirect introgression breeding.
Similarly, Hammenhag et al. [14] reconstructed the genomic architecture of recent ongoing domestication in field cress (Lepidium campestre), a promising oil crop for the subarctic. The authors genotyped 380 genotypes of an F₂ mapping population, and its F₃ progenies, for a total of 2330 GBS-derived SNP markers. This dataset allowed capturing nine quantitative trait loci (QTLs) linked with key domestication-related traits such as plant height, number of stems per plant, stem growth orientation, and perenniality.

2. Natural Adaptation Meets Breeding for Abiotic Stress Tolerance

Buitrago-Bitar et al. [15] perceptively explored allelic variation at three families of candidate genes (i.e., ASR [22], DREB [23], and ERECTA [24]) across naturally drought-tolerant legume resources from tepary bean (Phaseolus acutifolius), and its CWR. The team found that wild tepary offers a reservoir of unique alleles at genes for drought tolerance, surpassing conventional common bean (P. vulgaris) resources [25], as predicted for a species that originated in arid climates at the Mexico–USA border [26]. This research has already served as the foundation to counterbalance the domestication winnowing effect on natural genetic variation [27] via inter-specific crossing schemes [21].

However, a question remains open: how can we more efficiently unlock naturally available diversity from CWR and landraces as part of pre-breeding efforts? [28]. With this perspective in mind, novel genomic-based [29] strategies are reviewed here [16] to better utilize natural adaptation from CWR gene pools [30]. The authors argue that adaptation of CWR to hot and dry climates is indicative of how plants could respond to extreme weather [31]. Since natural selection has already tested more options than humans ever will [32], the review proposes (1) habitat-based population-guided samplings targeting unexplored semi-arid regions, and (2) geo-referencing-based environmentally coupled genetic characterizations of those collections [33,34]. The review ends prospecting last-generation ‘big data’ pipelines, such as genomic prediction [18], genomic-assisted back-crossing (GABC), speed breeding [10], and machine learning [35], all of which may help CWR boost pre-breeding for adaptation [36,37].

3. Meeting Future Demands

Balancing future nutritional [38] and bio-economical needs requires powering ‘big data’ [39] integrative trans-disciplinary strategies [40]. Precisely, all contributions to this Special Issue coincided with the need to merge the phylogenetic diversity [41], conservation efforts [42], and innovative utilization [43] of crop wild complexes to avoid plant resources becoming obsolete. Still, the bottlenecks promoting these synthetic approaches include the availability of open-source data [44], and consolidated research networks. In this sense, Cerón-Souza et al. [17] have called for a very timing moratorium to define guiding principles that could enhance research impact around plant genetic resources by bridging strong fragmentation and low connectivity among teams. The pillars of such discussion include the need to: (1) monitor and forecast gender and generation gaps to shrink disparity over time, (2) fund long-term synergies to leverage plant resources independent of market trends [45], (3) bridge plant germplasm resources with plant breeding [46], and (4) encourage joint training programs in last-generation technologies to speed up breeding cycles [18] and mitigate tradeoffs [47]. In parallel, it is necessary to find innovative bio-economical uses (such as was carried out by Hammenhag et al. [14]), and to (5) harness neglected or underutilized species [48] as a source of new [49] and future [37] crops (as envisioned by Buitrago-Bitar et al. [15] and Thapa et al. [13]). We look forward to seeing future research implementing these recommendations on crop–wild complexes [50–53].

Author Contributions: A.J.C., A.C. and R.Y. conceived this Special Issue, and jointly handled submissions. All authors have read and agreed to the published version of the manuscript.

Funding: A.J.C. thanks Vetenskapsrådet (VR) and Kungliga Vetenskapsakademien (KVA) for help conceiving this Special Issue through grants 4.1-2016-00418 and BS2017 0036, respectively.

Institutional Review Board Statement: Not applicable.
Informed Consent Statement: Not applicable.

Data Availability Statement: For original datasets, please refer to the published articles [13–17] within the Special Issue “Evolutionary Genetics of Plant Crop-Wild Complexes: From Fundamental to Applied Research” (https://www.mdpi.com/journal Genes/special_issues/Plant_Crop_Wild).

Acknowledgments: The guest editors want to acknowledge all authors, reviewers who made possible this Special Issue on “Evolutionary Genetics of Plant Crop-Wild Complexes: From Fundamental to Applied Research”. The editorial office at the Colombian Agricultural Research Corporation (AGROSAVIA) is thanked for divulgation.

Conflicts of Interest: The authors declare no conflict of interest.

References
1. Darwin, C. The Variation of Animals and Plants under Domestication; John Murray: London, UK, 1868.
2. Vavilov, N.I. The law of homologous series in variation. J. Genet. 1922, 12, 47–89. [CrossRef]
3. Purugganan, M.D.; Fuller, D.Q. The nature of selection during plant domestication. Nature 2009, 457, 843–848. [CrossRef]
4. Cornille, A.; Giraud, T.; Smulders, M.J.M.; Roldán-Ruiz, I.; Gladiieux, P. The domestication and evolutionary ecology of apples. Trends Genet. 2014, 30, 57–65. [CrossRef]
5. Meyer, R.S.; DuVal, A.E.; Jensen, H.R. Patterns and processes in crop domestication: An historical review and quantitative analysis of 203 global food crops. New Phytol. 2012, 196, 39–48. [CrossRef]
6. Meyer, R.S.; Purugganan, M.D. Evolution of crop species: Genetics of domestication and diversification. Nat. Rev. Genet. 2013, 14, 840–852. [CrossRef]
7. Purugganan, M.D.; Jackson, S.A. Advancing crop genomics from lab to field. Nat. Genet. 2021, 53, 595–601. [CrossRef]
8. Cortés, A.J.; Skees, P.; Blair, M.W.; Chacón-Sánchez, M.I. Does the genomic landscape of species divergence in Phaseolus beans cohere parallel signatures of adaptation and domestication? Front. Plant Sci. 2018, 9, 1816. [CrossRef] [PubMed]
9. Bitocchi, E.; Rau, D.; Bellucci, E.; Rodriguez, M.; Murgia, M.L.; Gioia, T.; Santo, D.; Nanni, L.; Attene, G.; Papa, R. Beans (Phaseolus spp.) as a model for understanding crop evolution. Front. Plant Sci. 2017, 8, 722. [CrossRef]
10. Varshney, R.K.; Bohra, A.; Roorkikwal, M.; Barmukh, R.; Cowling, W.A.; Chitikineni, A.; Lam, H.-M.; Hickey, L.T.; Crosier, J.S.; Bayer, P.E.; et al. Fast-forward breeding for a food-secure world. Trends Genet. 2021, 37, 1119–1132. [CrossRef] [PubMed]
11. Liu, S.; Cornille, A.; Decrooq, S.; Tricon, D.; Chague, A.; Eyquard, J.P.; Liu, W.S.; Giraud, T.; Decrooq, V. The complex evolutionary history of apricots: Species divergence, gene flow and multiple domestication events. Mol. Ecol. 2019, 28, 5299–5314. [CrossRef] [PubMed]
12. Burgarella, C.; Barnaud, A.; Kane, N.A.; Jankowski, F.; Scarcelli, N.; Billot, C.; Vigouroux, Y.; Berthouly-Salazar, C. Adaptive introgression: An untapped evolutionary mechanism for crop adaptation. Front. Plant Sci. 2019, 10, 4. [CrossRef]
13. Thapa, R.; Edwards, M.; Blair, M.W. Relationship of cultivated grain amaranth species and wild relative accessions. Genes 2021, 12, 1849. [CrossRef]
14. Hammehag, C.; Sariolla, G.V.; Ortiz, R.; Geleta, M. QTL Mapping for domestication-related characteristics in field cress (Lepidium campestre)—A novel oil crop for the subarctic region. Genes 2020, 11, 1223. [CrossRef] [PubMed]
15. Buitrago-Bitar, M.A.; Cortés, A.J.; López-Hernández, F.; Londoño-Caicedo, J.M.; Muñoz-Florez, J.E.; Muñoz, L.C.; Blair, M.W. Allometric diversity at abiotic stress responsive genes in relationship to ecological drought indices for cultivated tepary bean, Phaseolus acutifolius A. Gray, and its wild relatives. Genes 2021, 12, 556. [CrossRef]
16. Cortés, A.J.; López-Hernández, F. Harnessing crop wild diversity for climate change adaptation. Genes 2021, 12, 783. [CrossRef]
17. Cerón-Souza, I.; Gáleano, C.H.; Tehelen, K.; Jiménez, H.R.; González, C. Opportunities and challenges to improve a public research program in plant breeding and enhance underutilized plant genetic resources in the tropics. Genes 2021, 12, 1584. [CrossRef] [PubMed]
18. Desta, Z.A.; Ortiz, R. Genomic selection: Genome-wide prediction in plant improvement. Trends Plant Sci. 2014, 19, 592–601. [CrossRef]
19. Schrider, D.R.; Kern, A.D. Supervised machine learning for population genetics: A new paradigm. Trends Genet. 2018, 34, 301–312. [CrossRef]
20. Robert, C.P.; Gautier, M.; Corneil, J.-M.; Estoup, A.; Marin, J.-M.; Pudlo, P. Reliable ABC model choice via random forests. Bioinformatics 2016, 32, 859–866. [CrossRef]
21. Burbano-Erazo, E.; León-Pacheco, R.; Cordero-Cordero, C.; López-Hernández, F.; Cortés, A.; Tofío-Rivera, A. Multi-environment yield components in advanced common bean (Phaseolus vulgaris L.) × tepary bean (P. acutifolius A. Gray) interspecific lines for heat and drought tolerance. Agronomy 2021, 11, 1978. [CrossRef]
22. Cortés, A.J.; Chavarro, M.C.; Madriñán, S.; This, D.; Blair, M.W. Molecular ecology and selection in the drought-related Asr gene polymorphisms in wild and cultivated common bean (Phaseolus vulgaris L.). BMC Genet. 2012, 13, 58. [CrossRef] [PubMed]
23. Cortés, A.J.; This, D.; Chavarro, C.; Madriñán, S.; Blair, M.W. Nucleotide diversity patterns at the drought-related DREB2 encoding genes in wild and cultivated common bean (Phaseolus vulgaris L.). Theor. Appl. Genet. 2012, 125, 1069–1085. [CrossRef]
24. Blair, M.W.; Cortés, A.J.; This, D. Identification of an ERECTA gene and its drought adaptation associations with wild and cultivated common bean. Plant Sci. 2016, 242, 250–259. [CrossRef] [PubMed]

25. Cortés, A.J.; Blair, M.W. Genotyping by sequencing and genome—Environment associations in wild common bean predict widespread divergent adaptation to drought. Front. Plant Sci. 2018, 9, 128. [CrossRef]

26. Cortés, A.J.; Monserrate, F.; Ramírez-Villegas, J.; Madriñán, S.; Blair, M.W. Drought tolerance in wild plant populations: The case of common beans (Phaseolus vulgaris L.). PLoS ONE 2013, 8, e62898. [CrossRef] [PubMed]

27. McCouch, S. Diversifying selection in plant breeding. PLoS Biol. 2004, 2, 1507–1512. [CrossRef]

28. Tanksley, S.D.; McCouch, S.R. Seed banks and molecular maps: Unlocking genetic potential from the wild. Science 1997, 227, 1063–1066. [CrossRef]

29. Marks, R.A.; Hotaling, S.; Frandsen, P.B.; VanBuren, R. Representation and participation across 20 years of plant genome sequencing. Nat. Plants 2021, 11, 29. [CrossRef] [PubMed]

30. Zhang, H.; Mittal, N.; Leamy, L.J.; Barazani, O.; Song, B.-H. Back into the wild-Apply untapped genetic diversity of wild relatives

31. Varshney, R.K.; Barmukh, R.; Roorkiwal, M.; Qi, Y.; Kholova, J.; Tuberosa, R.; Reynolds, M.P.; Tardieu, F.; Siddique, K.H.M. Breeding custom—Designed crops for improved drought adaptation. Adv. Genet. 2021, 2, 3. [CrossRef]

32. Denison, R.F. Darwinian Agriculture: How Understanding Evolution Can Improve Agriculture; Princeton University Press: Princeton, NJ, USA, 2016.

33. Cortés, A.J.; López-Hernández, F.; Osorio-Rodriguez, D. Predicting thermal adaptation by looking into populations’ genomic past. Front. Genet. 2020, 11, 564515. [CrossRef]

34. Isabel, N.; Holliday, J.A.; Aitken, S.N. Forest genomics: Advancing climate adaptation, forest health, productivity, and conservation. Evol. Appl. 2020, 13, 3–10. [CrossRef] [PubMed]

35. Libbrecht, M.W.; Noble, W.S. Machine learning applications in genetics and genomics. Nat. Rev. Genet. 2015, 16, 321–332. [CrossRef] [PubMed]

36. Cortés, A.J.; Restrepo-Montoya, M.; Bedoya-Canas, L.E. Modern strategies to assess and breed forest tree adaptation to changing climate. Front. Plant Sci. 2020, 11, 583323. [CrossRef] [PubMed]

37. Bohra, A.; Kilian, B.; Sivasankar, S.; Caccamo, M.; Mba, C.; McCouch, S.R.; Varshney, R.K. Reap the crop wild relatives for past. Evol. Appl. 2020, 13, 3–10. [CrossRef] [PubMed]

38. Marks, R.A.; Hotaling, S.; Frandsen, P.B.; VanBuren, R. Representation and participation across 20 years of plant genome sequencing. Nat. Plants 2021, 11, 29. [CrossRef] [PubMed]

39. Zhang, H.; Mittal, N.; Leamy, L.J.; Barazani, O.; Song, B.-H. Back into the wild-Apply untapped genetic diversity of wild relatives

40. Cortés, A.J.; López-Hernández, F.; Osorio-Rodriguez, D. Predicting thermal adaptation by looking into populations’ genomic past. Front. Genet. 2020, 11, 564515. [CrossRef]

41. Gonzalez-Orozco, C.E.; Sosa, C.C.; Thornhill, A.H.; Laffan, S.W. Phylogenetic diversity and conservation of crop wild relatives in Colombia. Evol. Appl. 2021, 14, 2603–2617. [CrossRef]

42. Khoury, C.K.; Carver, D.; Greene, S.L.; Williams, K.A.; Achicanoy, H.A.; Schori, M.; Leon, B.; Wiersema, J.H.; Frances, A. Crop wild relatives of the United States require urgent conservation action. Proc. Natl. Acad. Sci. USA 2020, 117, 33351–33357. [CrossRef]

43. Migicovsky, Z.; Myles, S. Exploiting wild relatives for genomics-assisted breeding of perennial crops. Front. Plant Sci. 2021, 8, 460. [CrossRef] [PubMed]

44. McCouch, S.R.; Wright, M.H.; Tung, C.W.; Marion, L.G.; McNally, K.L.; Fitzgerald, M.; Singh, N.; DeClerck, G.; Agosto-Perez, F.; Korniliev, P.; et al. Open access resources for genome-wide association mapping in rice. Nat. Commun. 2016, 7, 10532. [CrossRef] [PubMed]

45. Guevara-Escudero, M.; Osorio, A.N.; Cortés, A.J. Integrative pre-breeding for biotic resistance in forest trees. Plants 2021, 10, 2022. [CrossRef]

46. Langridge, P.; Robbie, W. Harnessing the potential of germplasm collections. Nat. Genet. 2019, 51, 200–201. [CrossRef] [PubMed]

47. Dwivedi, S.L.; Reynolds, M.P.; Ortiz, R. Mitigating tradeoffs in plant breeding. iScience 2021, 24, 102965. [CrossRef]

48. Atchison, G.W.; Nevado, B.; Eastwood, R.J.; Contreras-Ortiz, N.; Reynel, C.; Madrinan, S.; Filatov, D.A.; Hughes, C.E. Lost crops of the Incas: Origins of domestication of the Andean pulse crop tarwi, Lupinus Mutabilis. Am. J. Bot. 2016, 103, 1592–1606. [CrossRef]

49. Von Wettberg, E.; Davis, T.M.; Smykal, P. Wild plants as source of new crops. Front. Plant Sci. 2020, 11, 591554. [CrossRef]

50. Debouch, D. Colombian Common and Lima Beans: Views on their Origin and Evolutionary Significance. Cienc. Tecnol. Agropecu. 1996, 1, 7–15. [CrossRef]

51. Gonzalez-Orozco, C.E.; Galán, A.A.S.; Ramos, P.E.; Yockteng, R. Exploring the diversity and distribution of crop wild relatives of cacao (Theobroma cacao L.) in Colombia. Genet. Resour. Crop Evol. 2020, 67, 2071–2085. [CrossRef]

52. Gonzalez-Orozco, C.E.; Porcel, M.; Rodriguez-Medina, C.; Yockteng, R. Extreme climate refugia: A case study of wild relatives of cacao (Theobroma cacao) in Colombia. Biodivers. Conserv. 2021, in press. [CrossRef]

53. Valencia, R.A.; Lobo Arias, M.; Ligarreto, G.A. State of Research of Plant Genetic Resources in Colombia: Germplasm Banks System. Cienc. Tecnol. Agropecu. 2010, 11, 85–94. [CrossRef]