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Variation under domestication in plants: 1859 and today

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Charles Darwin began *The Origin of Species* with a chapter entitled variation under domestication, which encapsulated decades of his research on a diverse array of animal and plant domesticated species. Variation in these species compared with that in their wild relatives, their origins and their selection by humans, formed a paradigm for his theory of the evolutionary origin of species by means of natural selection. This chapter, its subsequent expansion into a two-volume monograph, together with the rediscovery of Mendel's laws, later became the foundation of scientific plant breeding. In the period up to the present, several advances in genetics (such as artificial mutation, polyploidy, adaptation and genetic markers) have amplified the discipline with concepts and questions, the seeds of which are in Darwin's original words. Today, we are witnessing a flowering of genomic research into the process of domestication itself, particularly the specific major and minor genes involved. In one striking way, our view of domestic diversity contrasts with that in Darwin's writing. He stressed the abundance of diversity and the diversifying power of artificial selection, whereas we are concerned about dwindling genetic diversity that attends modern agriculture and development. In this context, it is paramount to strive for a deeper understanding of how farmer selection including both deliberate selection and unconscious selection, might generate and retain diversity. This knowledge is essential for devising *in situ* conservation measures.

Keywords: crop diversity; genomics; landraces; farmer selection; mutual evolution

1. INTRODUCTION

Darwin's chapter on variation in domesticated species of animals and plants holds the 'Genesis' opening position in '*The Origin of Species*'. On reflection, this is indeed remarkable. Many students of natural diversity disparage lessons from study of domesticates: species that exist at human behest, to feed, to clothe, to house or to transport us, or serve as cultural tokens. Surely, the science of the origin and maintenance of diversity in domesticated species cannot be extrapolated to diversity in nature? Yet, Darwin's thesis was that domesticated diversity displays the essential elements in the origin and evolution of species by natural selection. These are the mutability of species, the origin and phyletic relatedness of new diversity, and the nature of the selection process and progressive adaptation.

The chapter summarized the evidence for the transforming power of artificial selection in the origin of new breeds of animals and varieties of plants. This forms a paradigm and proof of concept for natural selection as the force adapting species to their environments and originating new ones. In 1868, a two-volume work, *The Variation of Animals and Plants under Domestication*, expanded the 'Origin' chapter to cover the improvement of plants and animals in agriculture (Darwin 1868). In two volumes, Darwin covered advances in an array of field crop, horticultural, livestock and pet species, the beneficial effects of crossing and the adverse effects of close inbreeding. He developed his hypothesis of pangenesis to fill the void of ignorance of how variation was inherited. This gap would be filled with the rise of genetics, generating an ever-burgeoning and rich field of research. Here, I note major themes concerning plant domesticate diversity in Darwin's treatment and compare them with those emerging today.

2. VARIATION UNDER DOMESTICATION AS PARADIGM, THE 1859 SUMMARY

(a) *Nature and extent of variability*

Darwin's opening statement is a resounding claim as to the great diversity present over space and time in the plant and animal species that humans have cultivated or raised. 'When we compare the individuals of the same variety or subvariety of our older cultivated plants and animals, one of the first points which strikes us is, that they generally differ more from each other than do the individuals of any one species or variety in a state of nature' (p. 5).[1]

He believed that this diversity arises from their being raised or grown under 'conditions of life' (p. 5) that are less uniform than, and different from those of the parent species. Darwin's many insights into variability were empirically based and individually are still amazingly apposite. However, the interpretation is made difficult by the confusion of variation in the phenotype as opposed to the genotype. From decades of experimenting and observing, he described diverse phenomena that we now label

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One contribution of 18 to a Discussion Meeting Issue 'Genetics and the causes of evolution: 150 years of progress since Darwin'.

Box 1. Darwin's pigeons—Origin and breed diversity.

Darwin's checklist of features of the pigeon (*Columba livia*) as an ideal study species. 'Believing that it is always best to study some special group, I have, after deliberation, taken up domestic pigeons' (p.15). How does your research organism compare with the humble pigeon?

- Darwin could and did raise all breeds.
- Collected extensively and exchanged specimens (skins).
- Read all treatises (in many languages).
- Joined fancier clubs and corresponded actively with breeders.
- Described characters thoroughly for all breeds.
- Reviewed wild-related species.
- Inter-crossed different breeds.
- Studied works from antiquity.

His main conclusions and insights

- 'The diversity of the breeds is something astonishing' (p. 15).
- 'At least a score of pigeons might be chosen … [which if an ornithologist] were told that they were wild, would be ranked by him as well-defined species' (p. 17). Some examples would be ranked as separate genera, especially when seen in clusters of sub-breeds or seeming species. In other words, pigeons demonstrate the hierarchical and correlated structure of variation.
- All breeds descended from one natural species (*Columba livia*). The diversity could question a single versus multiple ancestral wild species, suggesting that some putative progenitor species may now be extinct. However, the evidence argues for repeated domestications from one variable wild species.

His reasons for a single ancestral species

- Improbability of domesticating many species evident from the general difficulty of captive breeding of wild species.
- No other wild relatives known and none being anywhere feral.
- Breed characters are abnormal in the generic context (autapomorphic, not shared with any distant wild relatives).
- Reappearance of ancestral traits, 'both when kept pure and when crossed' (p. 20).
- Perfect fertility of hybrids. His hybrid experiments also gave transgressive segregation and re-appearance of ancestral wild characters.

In addition

- Wild *C. lavia* is 'found capable of domestication in Europe and India' (p. 20).
- An 'almost perfect series' (p. 20) is possible between extreme breeds.
- Distinctive breed characters are themselves eminently variable.
- 'Pigeons have been watched and tended with the utmost care, and loved by many people. … domesticated for thousands of years in several quarters' (p. 20). This accounts for 'the immense amount of variation which pigeons have undergone' (p 20).

Establishing *restricted if not unique origins* of domestication and subsequent diversification at the hands of humans was central to Darwin's logic. He was aware this often went against the specialist wisdom of the fancier. The expert maintained 'each main breed was descended from a distinct species' (p. 21). 'From long continued study (fanciers or breeders) are strongly impressed with the differences between several races;… win prizes from selecting slight differences, yet they ignore all general arguments, and refuse to sum up in their minds slight differences accumulated during many successive generations'. (p. 21).

as spontaneous mutation, segregation, plasticity or environmentally induced variation, genotype × environment interaction, accumulated modification and adaptation.

'Many laws regulate variation, some few of which can be dimly seen' (p. 8). While some such as the acquisition of induced characters loomed excessively in Darwin's field of vision, the phenomenon of correlated variation is still germane today. He cites breeders' use of indirect selection as evidence of the latter. 'Colour and constitutional peculiarities go together' (p. 9). Furthermore, selection will strongly reinforce the association between characters. 'If man goes on selecting, and thus augmenting, any peculiarity, he will almost certainly modify unintentionally other parts of the structure owing to the mysterious laws of correlation' (p. 9).

Variation in old cultivated plants (e.g. hyacinth, potato, dahlia) is extensive: … 'it is really surprising to note the endless points of structure and constitution in which varieties and subvarieties differ slightly from each other' (p. 9). 'Any variation which is not inherited is unimportant for us' (p. 9). 'The number and diversity of inheritable deviations, both … slight and considerable are endless' (p. 9). From the practical experience of plant breeders, from the resemblance between relatives and his own research, Darwin asserted that our basic view should be that '… the inheritance of every character whatever is the rule, and non-inheritance is the anomaly' (p. 10). Another major theme in Darwin's thoughts on descent with selective modification is the inevitable hierarchy of diversity: more closely related varieties are more alike than are distantly related ones.

Even allowing for confusion between genetic versus environmentally induced variation, Darwin's vision of abundant diversity is striking. There is no hint of diversity declining under domestication or being in danger of loss. It would take another century before genetic erosion became the urgent issue that it is today.

(b) *Divergence from progenitor wild species—the domestication process*

Darwin addressed questions concerning domestication that are still the focus of research today (Diamond 2002). These include the choice of species to domesticate, the number and location of domestication events, the number of 'aboriginal' species involved and the extent of divergence between varieties within species.

These questions arise when the process of domestication is posited as a paradigm of evolution in nature. What features distinguish the species that humans have chosen to domesticate? Was the choice biased towards 'plants having an extraordinary tendency to vary and likewise to withstand diverse climates' (p. 13)? But 'how could a savage possibly know...whether (a domesticated species) would endure other climates?' (p.13) He argued that if other species had been chosen, they would now resemble domesticates in patterns of variation. In contrast to the divergence between related species in nature, different varieties of the same crop species often differ from one another in 'an extreme degree in some part' (p. 12), when compared among varieties or between the cultigen and its wild relative. Aside from this point, Darwin argued that more generally, 'domestic races of the same species differ from each other in the same manner as do the closely-allied species of the same genus in a state of nature, but the differences in most cases are less in degree' (p.12).

The number of times, the number of species or lineages that are progenitors, and the geography of the events were all key issues. Whether ancient domesticates descended from one or more wild species was at that time difficult to tell. Darwin was aware of the potential of multiple events in several places repeated in time to give ample scope for the divergence of varieties. He wrote of 'a long continued previous period of less advanced civilisation, during which the domesticated animals, kept by different tribes in different districts, might have varied and given rise to distinct races' (p.13). Yet every true-breeding variety cannot have a separate wild progenitor, because of the number of such varieties. He queried if 'the crossing of a few aboriginal species' (p. 15) could be the source, because 'by crossing we can only get forms in some degree intermediate between their parents' (p. 15). Clearly, the most extreme forms could not be the wild progenitors. Greater insight into the possibilities of transgressive segregation would follow from the discovery of Mendel's laws.

The humble pigeon has a starring role in the chapter. What lessons does it hold for the student of domesticated plants? Box 1 summarizes its features in answer to this question.

(c) *Human selection*

Central to Darwin's understanding of diversity in domesticates are his conclusions on the 'principles of selection anciently followed' (subheading p. 22). 'One of the most remarkable features in our domesticated races is that we see in them adaptation, not indeed to the animal's or plant's own good, but to man's use or fancy. Some variations have probably arisen suddenly, or by one step' (p. 22). However, 'we cannot suppose that all the breeds were suddenly produced as perfect and useful as we now see them. ... The key is man's power of accumulative selection: Nature gives successive variations: man adds then up in certain directions useful to him' (p. 22).

The lifetime experience of eminent breeders, their ability to transform their flock, the market value of their new varieties (or pedigreed breeds, p. 23) and a common-garden comparative planting (p. 24) of different varieties attest to the reality and power of human deliberate selection. Progress under selection in horticultural plants is steady rather than in a single step and breeders 'go over their seed-beds, and pull up the 'rogues"(p. 24) to maintain a variety. Progressive divergence is not only achieved in breeders' characters, but also in other characters as well, because the 'law of *correlated variation*... will ensure some differences' (p. 24).

Darwin drew the distinction between deliberate or methodical selection in contrast to '*unconscious selection*' with a rich treasury of ideas that resonate currently in investigation of the maintenance of diversity on farms today. Methodical selection sustained over long periods towards minor improvements in a breed will in the longer term accumulate insensible changes. 'Change has been chiefly effected unconsciously and gradually' (p. 26), even while selecting to type. Furthermore, the stocks of one breed in the hands of different breeders diverge, even if unconsciously.

Unconscious selection is not the preserve of nineteenth century breeders, but he argued was also practiced by 'savages', ignorant of the rules of inheritance, and prone to 'famines and other accidents' (p. 26). Preferred individuals will 'leave more offspring than the inferior ones' (p. 26). Remarkably, Darwin noted that the varieties kept by savages ... have more of the character of true species, than the varieties kept in civilised countries' (p. 28). In facing famine and survival needs, selection also acted on humans for making correct choices. Darwin mentioned two conflicting human dynamics. 'It is in human nature to value any novelty, however slight'. (p. 28). Therefore, 'A man preserves and breeds from an individual' (p. 29) variant. Yet as well he tries 'to possess and breed from his best individual animals' (p. 25).

Anticipating the direction of current research in joining genetics with archaeology, Darwin cited works and authors from antiquity to show that humans for ages have long exploited deliberate selection to derive and maintain breeds and varieties and this is not a recent discovery '... the breeding of domestic animals was carefully attended to in ancient times .... It would indeed, have been a strange fact, had attention not been paid to breeding, for the inheritance of good and bad qualities is so obvious' (p. 25).

3. TRANSITION

Before leaping to the present, we set the scene with a mention of the major steps forward in genetics that shape the understanding of diversity in domesticates today.

They can be summarized conveniently into two epochs of about five decades each. The first resolved 'the laws governing inheritance [that] are for the most part unknown' (p. 10) (Richmond 2006). The relevant phenomena included the Mendelian genetic theory of inheritance, dominance and recessivity of characters, segregation of character-states, recombination or re-assortment of characters, the distinction between germ and soma and between genotype and phenotype, and the finding that chromosomes are the vehicles of the units of heredity. In developing his theory of pangenesis, Darwin summarized an array of empirical findings and experience, for which multiple segregating Mendelian factors can account.

By the time of the 'Origin's' centenary in 1959, other major advances in genetics had deepened our understanding of diversity. These included not only the discovery of DNA structure and the birth of molecular biology, but also, more immediate for plant breeders, advances in the use or knowledge of heterosis and inbreeding depression, artificial mutation, polyploidy, the evolution of ecotypes or biotypes within a species and germplasm collection (Müntzing 1959). The theory and practice of modern plant breeding were integrated and applied in this progress. Indeed Müntzing's detailed review pointed to the promise of breeding gains from the use of artificial mutations and induced polyploidy in breeding. In one influential plant breeding development, Suneson (1956) devised a bulk-population method that aimed to maximize unconscious selection for adaptedness, while restricting deliberate selection to crucial quality traits (Allard 1999, p. 176). The role of these synthetic heterogeneous populations (termed 'composite crosses') in breeding and in genetic resource conservation is still an area of research and debate.

4. TODAY

Molecular techniques, particularly large-scale DNA sequencing and expression microarrays, have heralded a new era of research on the evolution and diversity of domesticated plants (Doebley *et al*. 2006; Burke *et al*. 2007). Already a large and growing literature is beyond review here. A rich vein of new understanding of the genetics and evolution of field and horticulture crops is being tapped. One key area of research to stress here is that of the domestication process from wild progenitor to human-dependent crop. This area includes analysis of the genes involved, the consequences for linked and unlinked variability, the number of times and places domestication occurred and the introgressive inputs from other related species.

A second area involves research on the process of farmer selection as practised on farms. It has arisen from the mounting awareness of genetic erosion and the challenges involved in conserving crop genetic diversity *in situ* (Brown 2000). The aim of this research is to analyse the dynamics of crop diversity in the hands of those who husband it (Duputie *et al*. 2009).

(a) *Genomics of domestication*

Domestication is the outcome of a selection process that leads to the increased adaptation of plants or animals to cultivation or rearing and use by humans. The domesticate acquires improved fitness for human purpose often at the expense of survival in nature. A mutualistic relationship evolves between humans and their crops (Gepts 2004). Correlated changes in the genome can be divided into (i) predisposing phenomena, such as the occurrence of key mutations in morphological, phenological or utility genes that trigger or hasten the process and (ii) consequential phenomena, such as the loss of diversity, selective sweeps and adaptive diversification. A third group of possibly related genomic changes includes the divergence between contributing genomes in allopolyploids (e.g. rDNA genes in *Glycine*, Joly *et al*. 2004), or 'genomic coevolution' or homoeolog 'subfunctionalization' in *Gossypium* (Chaudhary *et al*. 2009) or retrotransposon-induced genome downsizing in rice (Ma *et al*. 2004). Such changes are neither necessary nor sufficient for the domestication process. They could contribute to the adaptability of a cultigen, but such changes occur in wild plant species and have been discovered in crop species mainly because, as Darwin argued, domesticated species are amenable research organisms (box 1).

Table 1 contains a sample of recent research or reviews that provide genetic evidence for several phenomena closely or loosely associated with domestication. Already the year 2009 has proven a bumper one for results and the growth of examples with contributions from several countries. Yet only a few of the major crops are featured. We may anticipate soon evidence from a wider range of species.

When many crop species each display the same trait or phenomenon, we can infer a link with domestication. The classic example is the evolution of a suite of traits labelled as the 'domestic syndrome' shared by several crops (Harlan 1992, p. 118: reviews in Gepts 2004, Doebley *et al*. 2006 and Panaud 2009). Another route for establishing the role of genetic phenomena in the evolution of domesticates and of the diversity they display is joint research with other fields such as archaeology, anthropology, socio-economics and traditional agronomy. Such research provides evidence that the attributes are targets of human selection. For example, Purugganan & Fuller (2009) link archaeological records for 'slow' progressive changes in two key traits of the cereal domestication syndrome (increasing grain size and loss of seed shattering) with changes in tools and cultivation practices. In highlighting an extended multi-stage process over millennia, the archaeological results contradict molecular studies that suggest rapid single origins.

(b) *Evolutionary dynamics of diversity on farms*

The second area of new perspectives on variation within domesticated plants is the evolutionary dynamics of diversity to be found currently on farms around the world. I believe an expanded, enriched and indeed Darwinian perspective is emerging on the role of humans in diversity husbandry as an

Table 1. Summary of examples of phenomena confirmed or discovered by molecular approaches with specific examples and sources.

research theme	crop species examples	result	references
number and location of domestication events	sunflower	events confined to a single region; crop-progenitor monophyly—repeated events	Rieseberg & Harter (2006)
	common bean	two centres—new world to old world intercontinental migration	Gepts (2004), Papa *et al.* (2006)
	rice	functional nucleotide polymorphisms (FNPs) in six domestication genes confirm two separate major centres for *indica* versus *japonica*	Izawa *et al.* (2009)
	10 grass species	repeated domestications in complex scenarios are common	Glémin & Bataillon (2009)
particular key loci	various	seven loci (five regulatory) associate with domestication; 18 (five regulatory) with varietal divergence	Doebley *et al.* (2006)
		frames the phenotype to genotype 'bottom-up' approach to finding new candidate loci	Ross-Ibarra *et al.* (2007)
	four grass species	10 loci tabulated, at least seven regulate expression at transcription	Glémin & Bataillon (2009)
multiple loci	maize	SNPs at 2–4% of 774 genes have responded to selection under domestication	Wright *et al.* (2005)
combining loci	rice	multiple selection steps	Izawa *et al.* (2009)
variation bottlenecks	maize	loss is uneven over the genome, highest for domestication loci. Modest population sizes only required to retain teosinte diversity	Buckler & Stevens (2006)
	rice	cultivated retain 70% of alleles in progenitor, and exhibit higher linkage disequilibrium (LD)	Li *et al.* (2009)
	wheat	estimated loss of 60% of SNP alleles for 21 loci (cf. 31% in lucerne)	Haudry *et al.* (2007)
	seven crops	estimates of diversity loss in the range 15%–95%	Glémin & Bataillon (2009)
selective sweeps	maize	a small 60–90 kb sweep 5-prime to *tb1*, the classic domestication locus, and no intergenic LD beyond	Clark *et al.* (2004)
		a large 1.1 Mb region of chromosome 10 with lost diversity	Tian *et al.* (2009)
	rice	a 260 kb region around *waxy* on chromosome 6	Purugganan & Fuller (2009)
genomic coevolution	cotton	based on 2177 arrays, gene expression diverges between homeologues	Chaudhary *et al.* (2009)
	wheat	non-additive microarray expression of homoeologous loci for 16% of genes	Pumphrey *et al.* (2009)

inextricably linked, interacting system, a mutualism in which diversity in human societies and communities interacts with diversity in the plants we tend. This view stresses the evolutionary dependence of the partners, a perspective that was previously used to describe host–parasite, host–pathogen or host–symbiont relationships.

Purugganan & Fuller (2009) have argued for applying the term '*coevolution*' to the crop–human mutualism. Coevolution is held to mean reciprocal evolutionary change in interacting species (Thompson 1994, p. 8). The coevolving species each adapt to changes in the other and thus act as agents of selection for each other. Evolutionary change and genetic diversification at human behest in crop plants are as given. However, on the human side, we need a deeper appreciation of human genetic and cultural evolution to match the expanding crop molecular data. Since cultural evolution is a much more evident and rapid process than genetic divergence in response to crop species evolution, the case for the term coevolution would rest on accepting its extension to include cultural diversification and change. Diamond (2002) instances human genetic evolution consequent on the population increase supported by domestication of plants and animals. In any case, such a usage is less precise than Darwin's own in treatment of the evolution of pollination specialization.

Along with Darwin (e.g. box 1), molecular geneticists (Doebley *et al.* 2006) have suggested, based on differences in classes of gene action, that conscious selection plays a greater role in diversification subsequent to domestication than in domestication itself. Yet the challenge in documenting farmers' selection criteria in relation to diversity is still relatively unmet. Thus of the 73 reports on factors controlling landrace genetic diversity in cereal and pulse crops that Teshome *et al.* (2001) reviewed, only 4/73 (5%) of studies had farmers' selection as their major focus. The remainder addressed biotic interactions (7/73 = 10%), abiotic stresses (10/73 = 14%), abiotic gradients (21/73 = 29%) and the catch-all 'geographical separation' (31/73 = 42%). It is important to establish how much of this geographical divergence arises from isolation by distance, as opposed to adaptive farmer selection, whether deliberate or unconscious.

Recently Jarvis *et al.* (2008) have synthesized data on the use of traditional varieties of 27 crop species in seven developing countries, to determine overall trends in varietal diversity on farms. They detected an overall close, curvilinear relationship between measures of varietal diversity richness (the number of varieties) and evenness (the relative lack of dominance of one or very few varieties). Such a relationship is a comparable construct to that for assessing DNA sequence diversity in searching for the footprint of selection (e.g. Wright *et al.* 2005; Tian *et al.* 2009) or of assessing species-community diversity patterns in line with 'neutral ecology' (Jarvis *et al.* 2008). It should provide a framework for specific hypotheses about farmer selection. For example, crop-community situations of high evenness might reflect multi-niche selection (separate divergent varieties for specialized uses or markets) or balancing selection (fields with more than one variety having more stable yields) and exemplify the use of diversity to meet immediate needs. In contrast, situations of high numerical dominance (low evenness) for a given richness suggest the retention of small amounts of the rarer varieties as insurance for future needs.

(c) *Farmer naming systems and mutual evolution*

Farmers' names are fundamental to the definition of traditional varietal diversity (Frankel *et al.* 1995, p. 57). In their study, Jarvis *et al.* (2008) used variety names to discern and overview global patterns of crop varietal diversity. The names that farmers use at a given locality and time and characters were as agreed by surveying local farming communities in a participatory approach. The approach aimed to identify the famers' units for managing diversity on farms (Sadiki *et al.* 2007; Jarvis *et al.* 2008), The procedure addressed the issue of the reliability of farmers' names, which some question as the basis of meaningful measures of diversity (see Nuijten & van Treuren 2007 for discussion of name homonyms and synonyms). Often such queries stem from surveys of large germplasm collections. Yet full consistency between names and genes should not be expected in such collections, owing to what Frankel *et al.* (1995, p.106) have called the 'vintage factor'. Collections are haphazard, historical, heterogeneous assemblages, garnered over decades from diverse sources, with variable handling. Indeed the relations between names and genes should evolve over time and space both *in situ* and *ex situ*.

As labels for suites of genotypes, names are likely to be labile in space and time and to evolve, reflecting one aspect of the cultural evolution that in humans is part of the mutual evolutionary process mentioned above. A Darwinian hypothesis for the importance of names recognizes that farmers make crucial decisions affecting life, based on such units of diversity. They will suffer directly the consequences of poor decisions, which is a worse outcome than that following an ecologist's misidentification of a species or having an erroneous species concept (e.g. one that lumps cryptic divergent genetic units). Indeed Brown & Brubaker (2000) speculate that the domestication process is likely to be self-reinforcing or self-fulfilling through Darwinian deliberate selection: the planting of a variety because farmers believe it to possess a specific tolerance or function will select that variety to acquire or strengthen the trait.

Thus, working at the level of names is crucial to opening up the analysis of socio-economic factors that maintain diversity *in situ* on farms. Deriving global inferences at the level of variety names provides specific hypotheses for the better focus of molecular methods. For example, Sadiki *et al.* (2007) cite published papers that test the relations between names and genetics for the crop populations that Jarvis *et al.* (2008) summarize.

5. CONCLUSIONS

The 1859 chapter ends with a section headed 'Circumstances favourable to Man's Power of Selection' (p. 29) that contains lessons for plant breeding and plant conservation genetics today. Progressive adaptation requires

- a 'high degree of variability' (p. 29), since diversity is obviously the raw material for selective advance. It is also the raw material for sustainability (Jarvis *et al.* 2007).
- a 'large number of individuals being kept' since 'useful or pleasing' variations are rare (p. 29). 'Number is of the highest importance for success.' (p. 29) Small lots typically belonging to 'poor people' are hard to improve. Numbers allow for selection, but 'when individuals are scanty, all will be allowed to breed ...' (p. 30).
- that selection is accurate, requiring the 'closest attention to even the slightest deviation in its qualities or structure'[2] (p. 30).
- 'facility in preventing crosses (which) is an important element in the formation of new races. ... In this respect enclosure of the land plays a part. Wandering savages or inhabitants of open plains rarely possess more than one breed ...'. (p. 30). (This insight arose from Darwin's success in co-housing many breeds of pigeons as monogamously pairing birds).

A low number of varieties points to 'selection not having been brought into play' (p. 30) (a lack of reproductive isolation, low population size, difficulties in culture, too few or limited uses, and 'no pleasure having been felt in the display of distinct breeds' (p.31), as well as species attributes).

Because of the speed and degree of selection response under domestication, Darwin argued it was wise to presume there is no limit to varietal diversification. He argued that diversity between varieties often exceeded that between congeneric species in nature, particularly for the characters attracting human attention (seed size, colour). Rather than bottlenecks at their birth setting the limit to crop diversity, it is modern human mismanagement of diversity that is a greater threat.

'To sum up on the origin of our domestic races of animals and plants' (p. 31): variability is crucial. The interaction of forces, *viz.* changed conditions of life, heritability, reversion, its correlated structure 'determine whether variations will endure' (p. 31). Species hybridization plays a varying role depending on breeding system. 'Overall these causes of Change, the accumulative action of Selection, whether methodically and quickly or unconsciously and slowly, seems to have the predominant Power' (p. 32, Darwin's upper case).

Out of more than 250 000 known plant species, only some 200 have been domesticated worldwide, of which only 20 crops provide most of the world food (Motley 2006). Are domesticated plant species too biased and specialized a sample? Have they outlived their paradigmatic role and are no longer needed for plant evolutionary studies? Recent advances in crop genomics and human selection indicate otherwise.

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ENDNOTES

[1] All quotations in this paper are from Darwin 1876 (Sixth edition with additions and corrections to 1872. Chapter 1).

[2] Darwin respected the achievements of stud breeders highly: 'Not one man in a thousand has accuracy of eye and judgement sufficient to become an eminent breeder' (p. 23). However, the same principle of the attention to detail applies to plant breeders, as Darwin specifically mentions for horticulturalists (p. 23).

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