Identifying genes and traits that have diverged during domestication provides key information of importance for maintaining and even increasing yield and nutrients in existing crops. A “bottom-up” population genetics approach was used to identify signatures of selection across the eggplant genome, to better understand the process of domestication. RNA-seq data were obtained for 4 wild eggplants (Solanum insanum L.) and 16 domesticated eggplants (S. melongena L.) and mapped to the eggplant genome. Single-nucleotide polymorphism (SNPs) exhibiting signatures of selection in domesticates were identified as those exhibiting high $F_{ST}$ between the 2 populations (evidence of significant divergence) and low $\pi$ for the domesticated population (indicative of a selective sweep). Some of these regions appear to overlap with previously identified quantitative trait loci for domestication traits. Genes in regions of linkage disequilibrium surrounding these SNPs were searched against the Arabidopsis thaliana and tomato genomes to find orthologs. Subsequent gene ontology (GO) enrichment analysis identified over-representation of GO terms related to photosynthesis and response to the environment. This work reveals genomic changes involved in eggplant domestication and improvement, and how this compares to observed changes in the tomato genome, revealing shared chromosomal regions involved in the domestication of both species.
The complicated demographics this produces can make it challenging to identify true wild and domesticated accessions based on phenotype alone. For example, Knapp et al. (2013) proposed a key to morphological characteristics for distinguishing ambiguous specimens; however, we recently showed that some phenotypically wild eggplants were in fact feral domesticates with admixed (wild and domesticated) genomes (Page, Gibson, et al. 2019). Analyses in eggplant aiming to identify variants associated with selection during domestication must therefore be accompanied by demographic inference such as a phylogeny to verify true wild and true domesticated accessions.

Previous work to identify the genomic regions underlying phenotypes in eggplants have largely taken a top-down approach, most often analyses of quantitative trait loci (QTL). These analyses have revealed loci linked to domestication traits using crosses between domestic and wild eggplant parents (Doganlar et al. 2002; Frary et al. 2014; Portis et al. 2014; Toppino et al. 2016; Miyatake et al. 2020), and loci controlling specific traits that vary between cultivars such as disease resistance (Barchi et al. 2018), and anthocyanin content (Barchi et al. 2012).

Domestication imposes a bottleneck on the crop, which increases the strength of genetic drift. This will lead to a genome-wide reduction in diversity. Regions of the genome which have been under selection will have lower diversity still, driving the selected allele and the fixation in diversity. Regions of the genome which have been under selection have had on the genome, such as what proportion of the genome is under selection, and whether the same regions were targeted in Solanaceous crops also reveals more about the effects artificial selection has had on the genome, such as what proportion of the genome was under selection, and whether the same regions were targeted in related crops.

Materials and Methods

Existing Datasets, RNA Extraction, and Sequencing

The RNA-seq data from Page, Gibson, et al. (2019) were reanalyzed in this work. We used the phylogenetic analysis of a genotyping-by-sequencing data set of 95 domesticated eggplants and wild relative species sampled across their range (Page, Gibson, et al. 2019) to define true wild and domesticated eggplants. True wilds are defined as wild accessions sister to the domesticates in the phylogeny, whereas phenotypically wild accessions nested within the domesticated clade with admixed genomes are defined as feral and are excluded here.

Briefly, one fully expanded leaf from each accession (4 wild and 16 domesticated; Table 1) was frozen in liquid nitrogen, and RNA was extracted using a Qiagen RNeasy Plant Mini kit (Qiagen, UK), utilizing an on-column DNase step (Qiagen). Samples were sent to the Wellcome Trust Centre for Human Genetics (WTCHG, Oxford, UK) for quantification, quality checking, and subsequent library preparation using Illumina’s Stranded Truseq kit (Illumina, UK). Up to 12 libraries (individually barcoded) were sequenced per lane on Illumina HiSeq2000 for 101 cycles (paired end). Samples were then demultiplexed and bioinformatic analyses took on the University of Southampton Iridis4 supercomputer. All samples are available from the NCBI Sequence Read Archive (PRJNA526115).

| Accession | Population | SRA accession | N reads | Country of origin | Spinesb | Fruit colorb | Fruit shapeb |
|-----------|------------|---------------|---------|-------------------|---------|-------------|-------------|
| MM12137   | Domesticated | SRR8736626    | 19 623 124 | India             |         |             |             |
| MM1712    | Domesticated | SRR8736644    | 11 685 753 | China             | No      | Purple      | Elongated   |
| MM1791    | Domesticated | SRR8736653    | 15 531 766 | Vietnam           | Yes (calyx) | Purple      | Round       |
| Mey319    | Domesticated | SRR8736652    | 26 896 589 | China             | No      | Purple      | Round       |
| PI241594  | Domesticated | SRR8736633    | 18 493 989 | Taiwan            |         |             |             |
| Arum      | Domesticated | SRR8736631    | 21 310 738 | India             |         |             |             |
| MM0609    | Domesticated | SRR8736630    | 12 326 452 | India             | No      | Purple      | Round       |
| MM0673    | Domesticated | SRR8736638    | 22 010 086 | India             |         |             |             |
| MM19439   | Domesticated | SRR8736627    | 23 224 957 | Maldives          |         |             |             |
| S00253B   | Domesticated | SRR8736636    | 22 806 997 | India             | No      | Purple      | Elongated   |
| S00392    | Domesticated | SRR8736637    | 22 688 619 | India             | No      | Purple      | Round       |
| MM12391   | Domesticated | SRR8736632    | 23 184 716 | Malaysia          | No      | Purple      | Round       |
| MM12454   | Domesticated | SRR8736635    | 23 079 041 | Indonesia         |         |             |             |
| MM1290    | Domesticated | SRR8736634    | 14 460 317 | Philippines       | No      | Purple      | Elongated   |
| MM1547    | Domesticated | SRR8736629    | 15 435 197 | Malaysia          | No      |             |             |
| PI470273  | Domesticated | SRR8736628    | 22 634 687 | Indonesia         | No      | Purple      | Round       |
| MM0669    | Wild         | SRR8736648    | 22 235 038 | India             | Yes     | Green       | Round       |
| MM0675    | Wild         | SRR8736647    | 18 680 378 | India             | Yes     | Green, variegated | Round |
| PI381155  | Wild         | SRR8736645    | 18 387 079 | India             |         |             |             |
| MM0686    | Wild         | SRR8736646    | 24 282 614 | Indonesia         |         |             |             |

Table 1. Samples from which RNA-seq data were used

Accession names beginning “MM” are from INRA, “Meyer” indicates collection of R. Meyer (UCLA), “PI” are from the USDA, “TS” and “S” are from the AVRDC. “ARUM” indicates a landrace from Amishland seeds.

Phenotypic information is given where available.
Transcriptome Variant Calling
RNA-seq reads were trimmed and poor quality bases and short reads removed using Trimmomatic v. 0.32 (Bolger et al. 2014) as described previously (Page, Gibson, et al. 2019), and aligned to the eggplant genome (Barchi et al. 2019) using STAR (Dobin et al. 2012). A gff3 file of predicted genes from the eggplant genome was supplied when indexing the genome with STAR, which improved mapping quality by providing annotations for known splice junctions. After mapping, Picard 2.8.3 (Broad Institute 2019) and GATK (McKenna et al. 2010) were used to process the mapped reads following the recommendations of GATK best practices for calling variants in RNA-seq, that is, marking duplicates in Picard, using SplitNCigarReads in GATK to split reads into exon segments, and calling variants with HaplotypeCaller in GATK. Hard filtering was then applied to the callset. GATK best practices recommend filtering clusters of 3 or more single-nucleotide polymorphism (SNPs) within a 35-base window, Fisher strand values > 30, and quality by depth values < 2. BCFtools within SAMtools v. 0.1.19 (Li et al. 2009) was used to merge the vcf files of samples into 2 files (wild and domesticated), then further filtering was done to remove any SNPs with a minor allele frequency (MAF) of <0.1, and with coverage in the lowest 99th percentile.

Population Genomic Statistics
The Populations program in Stacks v. 1.48 (Catchen et al. 2013), with the vcf files as input, was used to calculate AMOVA $F_{ST}$ between the domesticated and wild populations, and π within the domesticated population. SNPs were not filtered for missing data because of the small sample size in the wild population, which we assume adds some noise to the estimates of $F_{ST}$ and π. AMOVA $F_{ST}$ in Stacks was derived from Weir (1996) and was calculated as the weighted average of the surrounding 450 kb (the default value in Stacks) of sequence for each SNP. A weighted average of π in the surrounding 450 kb of sequence was also calculated for the domesticated population. 10^6 bootstrap replicates were performed and used to report P values, which were subsequently corrected using the Holm–Bonferroni sequential correction (Holm 1979), calculated using the p.adjust command in R 3.1.3 (R Core Team 2015) on a per chromosome basis. These were considered outlier SNPs for high $F_{ST}$, low π, and their overlap.

Gene Ontology Analysis
A fasta file containing the sequences of all annotated genes in the regions putatively under selection was created from the eggplant genome sequence using gff3 files to identify genomic positions. This fasta file was used in a BLAST search against Arabidopsis thaliana CDS sequences (ver. TAIR10) and tomato (ver. ITAG2.4) using Bioedit (Hall 1999), retaining significant hits (e-value < e^{-10}). These lists of genes were then used in a gene ontology (GO) enrichment analysis (Ashburner et al. 2000) with agrigo (Du et al. 2010) to identify GO terms that were over-represented in the candidate gene list. False discovery rate correction was applied to the P-values.

Results
Mapping and Calling SNPs
Between 11.7 and 26.9 M reads were sequenced from each accession, with an average of 19.9 M (± 0.9 M [SE]). Annotated coding genes make up 8.90% of the 1.2 Gb eggplant genome, and of the 27 139 annotated coding genes in the eggplant reference genome, 22 954 were present in the transcriptome of at least one accession. Following hard filtering on the SNPs called, the average number of SNPs per sample decreased by 10.73%, from 117 699 to 105 075. After merging samples based on population, further filtering on MAF and coverage retained 203 611 out of a possible 668 552 SNPs.

Haplotype Block Analysis to Estimate the Average LD in the Eggplant Genome
When the upper-class boundary of the estimated haplotype block sizes, estimated for the combined wild and domesticated data, was plotted against the cumulative percentage, there was a clear drop off in the rate of increase of haplotype block size (Figure 1). The
The majority of haplotype blocks (72.5%) are under 3.93 Mb in size, and following this point, increasing the length of block has diminishing returns for the increase in the cumulative percentage of haplotype blocks. Therefore, 3.93 Mb was used to define the region of interest around loci with significant \( F_{ST} \) and/or \( \pi \).

**Regions of the Genome Under Selection**

After combining significant SNPs within 3.93 Mb as potentially in LD and therefore marking the same region of the genome, 6 genomic regions with significantly (adjusted \( P < 0.05 \)) low \( \pi \) in domesticates were identified (on chromosomes [chr] 1, 2 [2 regions], 4, 6, and 9) and 3 with significantly (adjusted \( P < 0.05 \)) high \( F_{ST} \) were detected (on chr 2, 6, and 9; Table 2; Figure 2). The low \( \pi \) and high \( F_{ST} \) regions on chr 9 overlapped almost completely, whereas the others did not. There are other peaks in \( F_{ST} \), such as at the ends of chr 1, 3, and 8, and a highly heterogeneous distribution of \( \pi \) but these are not statistically significant. These 8 regions totaled ca. 63 Mb, approximately 5.6% of the eggplant genome and contained between 39 and 526 (mean 178.75) annotated genes. Of these, 375 had a significant \((\epsilon \text{-value} < e^{-15})\) BLAST hit in Arabidopsis and 1113 had a significant BLAST hit in tomato (Supplementary Table 1). None of the putative orthologs had clear functions related to domestication traits in eggplant. In addition, we identified the genomic coordinates of molecular markers under the QTL peaks from the Doganlar et al. (2002) study and the prickliness indel marker from Miyatake et al. (2020) (Supplementary Table 2). In only one case was there overlap with a selective sweep; this was for the shoot anthocyanin QTL sa6.1 which overlapped with sweep 6_2 on chr 6.

**GO Analysis Reveals Putative Selection on the Photosynthetic Pathway**

A GO analysis using the combined list genes in the 8 genomic regions putatively under selection was carried out, revealing significant \((P < 0.05 \text{ after false discovery rate correction})\) over-representation for 171 GO terms (Supplementary Table 3). Many of the over-represented GO terms are related to photosynthesis, including *photosynthesis, photosystems I and II, chlorophyll and chloroplasts, thylakoids, plastids, and tetrapyrrole binding*. This included the putative orthologs of genes *PsbO-1 (PS II oxygen-evolving complex)* and *LHCB3 (light harvesting complex of photosystem II S)*, both of which are involved in photosystem II assembly (Jansson 1999; Popelkova and Yocum 2011).

Other terms involved in response to the environment including *response to osmotic stress* and *response to salt stress* as well as *response to hormone stimulus* were also uncovered.

**Discussion**

In this study, measures of population differentiation between wild and domesticated populations of eggplants and nucleotide diversity within the domesticated population were used to identify genomic regions having the signature of selection during domestication.

Using our pipeline, identifying haplotype blocks in which outlier SNPs were found, we find that genomic regions putatively under selection during eggplant domestication were few in number and are each relatively small in size, ranging between 7.8 and 8.3 Mb and are found on 5 of the eggplant chromosomes (chr 1, 2, 4, 6, and 9).

In total, this comprises about 5.6% of the eggplant genome; a similar analysis in tomato, but based on different methods to identify regions under selection, suggested about 1% of the genome was under strong selection (Sahu and Chattopadhyay 2017). That a small portion of the genome is shown to be under selection fits with the observation from QTL studies that in general a small number of QTL control domestication traits (Paterson 2002). For example, in maize, a small number of large effect genetic variants appear responsible for the transition from wild teosinte, whereas variants with smaller effects were responsible for improvement traits that contribute to standing variation in maize crops (Xue et al. 2016).

Eggplant and other members of the Solanaceae exhibit extensive chromosome-level synteny (Wu et al. 2009), so regions under selection can be compared. Indeed, it has already been reported that the QTL on chr 2 and 4 discussed above overlap with QTL for similar traits in tomato and pepper (Doganlar et al. 2002). Comparing our regions of selection to QTL maps for eggplant (Doganlar et al. 2002; Frary et al. 2003), it appears that regions on chr 2 and 4 may correspond to regions of the eggplant genome controlling fruit size and on chr 6 these regions may correspond to regions of the genome controlling prickliness and/or anthocyanin content. We attempted for test for overlap by looking for molecular markers closest to the QTL peaks in the Doganlar et al. (2002) study, and we did not find these markers in our selective sweeps (with one exception; see Results); however, sometimes the sweep and QTL region appeared close, and given that the QTL sometimes spanned 5–15 cM, there is possible overlap, even if the peaks do not coincide. We also note that the landraces are morphologically diverse and so we might not expect our comparison (wild vs. domesticated) to identify, for example, loci associated with fruit color or shape, given these are very variable in the landraces.

These regions collectively contained 1430 annotated genes, of which ca. 26% had a hit in the Arabidopsis genome and 78% had a hit in the tomato genome. GO enrichment analysis can reveal patterns in selection pressures and can be particularly useful when processing large lists of candidate genes. Using this, we found genes with orthologs related to photosynthesis were

| Table 2. Genomic regions of low diversity (low \( \pi \) in domesticated) or high differentiation (high \( F_{ST} \)) in the comparison of the wild and domesticated eggplant populations |
|----------------|----------------|----------------|--------|---------------------------------|--------|
| Region name    | Test   | N sig SNPs | Chr   | Position | N genes |
| 1_1            | \( \pi \) | 3          | 1     | 10 7962 400–11 5824 939 | 73     |
| 2_1            | \( \pi \) | 2          | 2     | 13 892 778–22 201 207 | 54     |
| 2_2            | \( \pi \) | 6          | 2     | 60 392 355–68 261 479 | 39     |
| 2_3            | \( F_{ST} \) | 6         | 2     | 69 739 198–77 677 099 | 285    |
| 4_1            | \( \pi \) | 5          | 4     | 42 196 297–50 056 466 | 53     |
| 6_1            | \( \pi \) | 5          | 6     | 79 014 216–86 874 666 | 179    |
| 6_2            | \( F_{ST} \) | 2         | 6     | 92 198 368–10 013 870 | 526    |
| 9_1            | \( \pi \) and \( F_{ST} \) | 16       | 9     | 5 546 492–13 498 317 | 221    |
significantly over-represented in the regions showing a signal of selection. Photosynthesis is a pathway that has been identified as under selection in a number of crops including tomato (Koenig et al. 2013), other fruit crops (Cao et al. 2014; Li et al. 2019), and nonfruit crops (Pujol et al. 2008; Akakpo et al. 2017), and that has been suggested as a target for crop improvement (Long et al. 2015).

There is no consistent pattern in the change in photosynthetic rate in domesticated species relative to their wild relatives. Increase in photosynthetic rate was observed in domesticated rice (Cook and Evans 1983), soybean (Li et al. 2013), and cassava (Pujol et al. 2008), whereas photosynthetic rate and photosynthetic pigments were found to be reduced in domesticated yam relative to the wild progenitor (Padhan and Panda 2018). As domestication often involves a move from a nutrient poor to a nutrient rich habitat, an increase in photosynthetic rate can allow a domesticated species to grow more rapidly in a more protected and nutrient rich environment provided by human cultivation (Pujol et al. 2008). Photosynthetic capacity has been identified as one of the most important targets for increasing crop yield (Long et al. 2015) but has largely been under represented in crop improvement, perhaps due to the complexity of the genetics and the molecular mechanisms controlling traits related to photosynthesis (Mathan et al. 2016). As far as we are aware, photosynthetic rate has not been measured in wild and domesticated eggplant. Quantifying this will be an important next step to understanding the evolution of the photosynthetic pathway during domestication in eggplant.

Conclusions

Sequencing the transcriptome is an effective way of reducing the complexity of the genome, making genome-scale analysis more computationally and cost efficient. However, this approach also comes with the caveat that only expressed genes will be sequenced; for example, in our recent work, we identified targets of selection on a gene-by-gene basis using transcriptome sequencing (Page, Gibson, et al. 2019), which would preclude the sequence analysis of nonexpressed or differentially expressed loci. In the present study, by mapping the expressed genes to the genome, we overcome this shortfall by identifying SNPs exhibiting signatures of selection (from transcriptome sequencing) and then interrogate the entire genomic region for candidate genes. Some of these signals of selection appear to overlap with previously identified domestication-related QTL, and we show that genes in these regions are enriched for functions related to photosynthesis, which is a relatively under-recognized and understudied domestication trait that has been linked to yield increase in cassava and fruit ripening in tomato.

Supplementary Material

Supplementary data are available at *Journal of Heredity* online.

Supplementary Table 1. Gene names, taken from the eggplant genome gff files, and top Arabidopsis (A) and tomato (B) hits in the regions under selection.

Supplementary Table 2. QTL locations and potential overlap with selective sweep regions.
Supplementary Table 3. Over-represented GO terms in regions showing a signal of selection. P=biological process. F=molecular function, C=cellular component.

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Data Availability
RNA-seq data are available from the NCBI SRA under accession numbers SRR8736626–SRR8736638, SRR8736644–SRR8736648, SRR8736652, and SRR8736653.

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