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**Discovery of ongoing selective sweeps within *Anopheles* mosquito populations using deep learning**

Short title: Classifying partial sweeps in *Anopheles* populations via deep learning

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## Abstract

Identification of partial sweeps, which include both hard and soft sweeps that have not currently reached fixation, provides crucial information about ongoing evolutionary responses. To this end, we introduce a deep learning approach that uses a convolutional neural network for image processing, which is trained with coalescent simulations incorporating population-specific history, to discover selective sweeps from population genomic data. This approach distinguishes between completed versus partial sweeps, hard versus soft sweeps, and regions directly affected by selection versus those merely linked to nearby selective sweeps. We perform several simulation experiments under various demographic scenarios to demonstrate the performance of our deep learning classifier *partialS/HIC*, which exhibits unprecedented resolution for detecting partial sweeps. We also apply our method to whole genomes from eight mosquito populations sampled across sub-Saharan Africa by the *Anopheles gambiae* 1000 Genomes Consortium, elucidating both continent-wide patterns as well as sweeps unique to specific geographic regions. These populations have experienced intense insecticide exposure over the past two decades, and we observe a strong overrepresentation of sweeps at insecticide resistance loci. Our analysis thus provides a catalog of candidate adaptive loci that may aid mosquito control efforts. More broadly, the success of our supervised machine learning approach introduces a powerful method to distinguish between completed and partial sweeps, as well as between hard and soft sweeps, under a variety of demographic scenarios. As whole-genome data rapidly accumulate for a greater diversity of organisms, *partialS/HIC* addresses an increasing demand for useful selection scan tools that can track in-progress evolutionary dynamics.

# Author Summary

Recent successful efforts to reduce malaria transmission are in danger of collapse due to evolving insecticide resistance in the mosquito vector *Anopheles gambiae*. We aim to understand the genetic basis of current adaptation to vector control efforts by deploying a novel method that can classify multiple categories of selective sweeps from population genomic data. In recent years, there has been great progress made in the identification of completed selective sweeps through the use of supervised machine learning (SML), but SML techniques have rarely been applied to partial or ongoing selective sweeps. Partial sweeps represent an important facet of evolution as they reflect present-day selection and thus may give insight into future dynamics. However, the genomic impact left by partial sweeps is more subtle than that left by completed sweeps, making such signatures more difficult to detect. To this end, we extend a recent SML method to partial sweep inference and apply it to elucidate ongoing selective sweeps from *Anopheles* population genomic samples.

# Introduction

Malaria represents an enormous burden on human health, with an estimated 214 million cases and 438,000 deaths in 2015 [1]. As mosquitos of the *Anopheles gambiae* species complex are the major vector for *Plasmodium* parasites, roughly 70% of global malaria relief budgets have been focused on mosquito control, including insecticide treated bed-nets, indoor residual spraying, and larva control through the direct modification of habitats as well as the application of larvicide. While these vector control efforts have successfully produced major reductions of malaria transmission rates over the past 15 years [1], there has been an alarming increase in mosquitos resistant to insecticides, specifically pyrethroids, observed across nearly all areas of the world covered by anti-malarial efforts [2]. Pyrethroids are the only class of insecticide used in long-lasting insecticidal nets and are applied in many indoor spraying programs, thus the evolutionary innovation of resistance is a well-recognized Achilles heel of anti-malarial efforts.

The increase in insecticide resistant mosquitoes is to be expected from an evolutionary standpoint: anti-malaria control efforts exert a strong selective pressure to which mosquito populations will respond through the differential survivorship and reproduction of those individuals that can best cope with the applied insecticides. Pyrethroid resistance was reported within African malaria vectors first in Sudan during the 1970s, then later in West Africa during the 1990s, most likely stemming from accidental exposure of mosquitos to crop applications of pyrethroids [3,4]. Subsequent analysis showed this earliest resistance to be a result of mutations in the knockdown resistance locus *kdr*, which is known to contribute to pyrethroid resistance in other insect species [5]. Mutations conferring resistance at *kdr* as well as other loci have since spread throughout Africa, and threaten to nullify the gains in malaria control achieved over the past decade [6]. While control efforts are now looking toward non-pyrethroid insecticides [2,7] as well as gene drive technologies [8], it is anticipated that resistance to these control modalities will eventually evolve as well [9,10]. Hence, an important goal in the continued fight against malaria is to identify genomic targets of resistance in *Anopheles*, especially in such a way that might inform vector managers in the field.

Alleles that confer resistance to control efforts should rapidly increase in frequency
within *Anopheles* populations in a manner consistent with selective sweeps. When an allele
increases in frequency under selection, its linked genetic background comes with it in a
process known as genetic hitchhiking. Selective sweeps, through this hitchhiking effect,
lead to decreased levels of polymorphism [11–13], skewed allele frequency spectra [14,15],
and increases in linkage disequilibrium surrounding the site under selection [16].
Classically, methods for finding sweeps have focused on a particular aspect of genetic
variation, for instance observing the site frequency spectrum (SFS) at a locus and
comparing it to expectations under neutrality and selective sweeps [19]. More recently, the
field has made excellent progress in combining signals across multiple features of genetic
variation through supervised machine learning (SML) [20–27], which has substantially
improved power, accuracy, and robustness in what have been stubbornly difficult inference
problems within population genetics [28]. While much attention has been paid to applying
SML for the identification and classification of completed selective sweeps in the genome
[24,26], less effort has been made for using SML to identify sweeps that are incomplete
within a population, sometimes called partial sweeps (although see Sugden *et al.* [27] for a
recent example). In these cases, the beneficial allele is not currently fixed within the
population, thereby creating a weaker hitchhiking effect in comparison to a completed
sweep, and accordingly a more subtle perturbation of patterns of genetic variation [29].
Partial sweeps may perhaps be implicated in cases where recently initiated selective forces
cause presently ongoing adaptation, directional selection ceases prior to fixation, or an
intermediate allele frequency is favored by balancing, polygenic, and/or pleiotropic
selection.

Here we introduce *partialS/HIC*, an extension of *S/HIC* [24] and *diploS/HIC* [26] that
includes both hard and soft partial sweeps along with their associated linked classes (*i.e.*
regions adjacent to either a partial hard or soft sweep) as selection states for which a
genomic window can be classified. We apply our extended method to data from phase I of
the *Anopheles gambiae* 1000 genomes project (Ag1000G) [6], with particular emphasis on
discovering sweeps currently in progress that might be the result of vector control efforts
such as insecticide spraying. We find that our method is considerably more powerful for

finding partial sweeps than *iHS* [30], even in the face of complex population size histories

such as those found among the Ag1000G samples. Application of our method to the

Ag1000G data reveals a large number of partial sweeps as well as completed sweeps from

standing genetic variation. Moreover, we find that our sweep candidates are highly

enriched for loci that have been previously identified as contributing to insecticide

resistance.

# Results

***Figure 1. Flowchart of methodological procedure.*** *Major steps highlighted in green. Note*
*that processing of simulated data incorporated uncertainties within the empirical data,*
*specifically with respect to masking sites from calculation of summary statistics.*

## Coalescent simulations of feature vector images for *partialS/HIC* training

We aimed to classify genomic segments into one of nine states: unaffected by selection (*i.e.*

neutral); containing a completed hard, completed soft, partial hard, or partial soft sweep,

respectively; or linked to a completed hard, completed soft, partial hard, or partial soft

sweep, respectively (Figure 1). To this end, we developed *partialS/HIC*, a SML classifier that

uses a deep convolutional neural network (CNN) to classify a genomic window, which is

represented by a two-dimensional matrix constructed from a large collection of summary

statistics. To train *partialS/HIC*, we deployed the program *discoal* [31] to perform

coalescent simulations of completed and partial as well as hard and soft selective sweeps,

along with simulations without sweeps, in a manner analogous to Schrider and Kern [24].

This was conducted for each of eight population size histories corresponding to the

empirical Ag1000G population datasets, which were previously inferred as part of the

initial data release [6]. These *Anopheles* population datasets from Miles *et al.* [6] are labeled

here as AOM (*A. coluzzii* from Angola), BFM (*A. coluzzii* from Burkina Faso), BFS (*A.*

*gambiae* from Burkina Faso), CMS (*A. gambiae* from Cameroon), GAS (*A. gambiae* from

Gabon), GNS (*A. gambiae* from Guinea), GWA (*Anopheles* of uncertain species from Guinea-

Bissau), and UGS (*A. gambiae* from Uganda). Individual simulations were converted into

two-dimensional matrices, or feature vector images, built from 89 rows corresponding to

different summary statistics, and 11 columns corresponding to adjacent sub-windows. The

89 statistics include 17 that are implemented in *diploS/HIC* along with 72 derivatives of the

recently developed SNP-specific SAFE statistic [32]. We defined the four completed

hard/soft and partial hard/soft selective sweep states as containing a sweep within the

central, focal sub-window. In contrast, the four linked selection states were defined as

having a sweep of the given type within one of the remaining ten sub-windows. Heatmaps

constructed from median values across simulations reveal expected spatial patterns, such

that values immediately flanking a sweep are substantially different than those further

from the focal sub-window, while neutral regions display no discernible pattern among

sub-windows (Figure S1). Additionally, spatial patterns of statistics differ qualitatively

between selection states. These observations are consistent regardless of mosquito

population history, suggesting that there is signal within this collection of summary

statistics to isolate the location of a sweep to a specific sub-window as well as distinguish

among neutral regions and types of selective sweeps.

## Deep learning excels in detecting selective sweeps, including partial hard sweeps

*Figure 2. CNN architecture of neural network layers. The input feature vector image is passed to a 2D convolutional layer with 256 filters using a 3×6 receptive field. Next is a 2D max pooling layer given a 3×3 receptive field. Then there is a second 2D convolutional layer of 256 filters based on a 3×3 receptive field and ReLU activation. Afterward is a second 2D max pooling layer, also with a 3×3 receptive field. The tensor is then flattened and passed to two fully-connected layers with ReLU activation, resulting in 512 and 128 nodes respectively. Finally, a softmax activation layer classifies the 9 responses.*

We utilized *partialS/HIC* to train a separate CNN for nine-state classification on each of the eight demographic histories associated with the Ag1000G population samples (Figures 1–2). In order to assess accuracy, each CNN was subsequently tested against another set of simulated data that was generated under the same specifications as the training dataset. Among the eight test sets, there was moderate overall accuracy for this simulation experiment (median accuracy = 66.4%; Table S1). However, confusion matrix heatmaps provide a more informative view of our classifier's performance, which was generally sufficient for identifying neutral regions, completed hard and soft sweeps, partial hard sweeps, and regions linked to completed hard/completed soft/partial hard sweeps (Figures 3, S2). Assignment accuracy was highest for completed hard sweeps in all demographic scenarios save for AOM (median accuracy = 96.0%). We also had excellent accuracy for identification of linked completed hard regions, demonstrating a strong ability to localize completed hard sweeps. Accuracy for completed soft sweeps was also quite good (median accuracy = 84.2%); when misclassification did occur, it was generally to either the

neutral or partial soft sweep state, thus completed soft sweeps were rarely incorrectly
classified as hard sweeps. Moreover, sub-windows linked to completed soft sweeps beyond
one sub-window away had low levels of misclassification to one of the non-linked sweep
states, again allowing for excellent localization of the sweep.

Importantly, the purpose of *partialS/HIC* is to extend our state space to identify
ongoing selective sweeps while distinguishing these from completed sweeps. We find that
our ability to identify partial hard sweeps was generally strong across population histories
(median accuracy = 74.6%) and is often comparable to that of completed soft sweeps.
However, localization of partial hard sweeps along the chromosome was more difficult
than for completed sweeps, as can be seen from the moderate levels of confusion between
partial hard sweep and linked partial hard sweep sub-windows. Undoubtedly, this is due to
the limited amount of time recombination has had to whittle down the haplotype carrying
the beneficial mutation.

Identifying partial soft sweeps was a much more challenging task (median accuracy
= 45.3%), with a high false negative rate (median rate of misclassification as neutral =
27.6%) as well as a substantial probability of misclassification as a completed soft sweep
(median rate = 14.4%). It is encouraging though that partial soft sweeps were almost never
misclassified as a completed nor partial hard sweep. Additionally, while our accuracy in
classifying partial soft sweeps was poor, false positives were not a substantial concern
(median rate of misclassifying neutral regions as partial soft sweep = 3.2%). Therefore,
*partialS/HIC* should underestimate the true number of partial soft sweeps when applied to
a given dataset. Furthermore, linked partial soft sweeps beyond one sub-window away
from the focal sub-window were rarely mistaken for a sweep state, and likewise partial soft
sweeps were seldom confused for being linked (median rate of misclassification as linked
partial soft sweep = 4.3%), thus demonstrating that localization of partial soft sweeps may
be possible.

In summary, *partialS/HIC* has excellent ability to distinguish partial from completed
sweeps for *de novo* mutations, and lesser yet still substantial power for sweeps from
standing variation. Moreover, we demonstrated very strong performance in differentiating

between hard and soft sweeps, regardless of whether a sweep was completed or incomplete. Importantly, this is all while maintaining an acceptable false positive rate across each of the population histories tested (median accuracy for neutral regions = 85.1%; median rate of misclassifying neutral regions as any one of the four non-linked sweep states = 4.6%).

*Figure 3. Confusion matrix heatmap of simulation experiment including partial sweep training.* Given the BFS population history.

## Robustness to demographic model misspecification

To assess robustness to demographic misspecification, we applied a CNN trained on simulations from one population sample to data generated from an alternate demographic

history (Figure 1). Specifically, we used training data from the GAS population size history,
which was fairly stable over time, and leveraged it against the CMS test dataset, which
experienced a dramatic population expansion (overall accuracy = 55.0%; rate of
misclassifying neutral regions as any one of the four non-linked sweep states = 1.7%).
Despite this misspecification, the confusion matrix (Figure S3) strongly resembles the
corresponding matrix that is correctly specified for demography (*i.e.* for CMS in Figure S2).
In particular, accuracies for finding neutral regions, completed hard sweeps, and partial
hard sweeps are roughly equivalent between the correctly specified model and
misspecified model (Figure S3). For soft sweeps, while confusion between completed and
partial sweeps is increased for the misspecified model, the overall ability to distinguish
sweeps from neutrality is largely preserved. Moreover, the rates at which examples from
the linked classes were mistaken for sweeps are seemingly unaffected. Together, these
results indicate that sensitivity for sweep discovery and localization was not strongly
impacted by the demographic model misspecification during training.

## Partial sweeps are unpredictably misclassified as either completed sweep or neutral when not explicitly considered

Since the previous versions of *partialS/HIC* (*S/HIC* and *diploS/HIC*) did not allow for partial
sweep selection states, we were interested in how such five-state classifiers would behave
when confronted with partial sweeps. To explore this, we conducted a simulation
experiment that first removed partial hard and soft sweeps as well as their associated
linked classes from the CNN training process, thus training on only five states rather than
all nine (Figure 1). Next, in an effort to examine the classification behavior for these five-
state CNNs, we applied the full test set that included the partial sweep classes.
Unsurprisingly, the trend was for partial sweeps to be most often confused for linked
selection (Figures 4, S4). Perhaps more concerning is the false negative rate (*i.e.* rate at
which partial sweeps were misclassified as neutral), which was substantial in partial hard
sweeps for several populations (median = 8.8%; max = 32.4%; >1% in all populations) and
extreme in partial soft sweeps (>50% in three populations, >40% in three more

populations, and >24% in all populations). Partial hard sweeps that were discovered were

also often misclassified as a completed soft sweep (median rate of misclassification as

completed soft sweep = 5.5%). However, when training included partial sweeps, there is

universal and dramatic improvement in both finding sweeps and correctly identifying the

model of selection (Figures 3, S2). Meanwhile, overall accuracy remains similar among the

five-state and nine-state classifiers with respect to simulations of neutral, completed

sweep, and linked classes exclusively (Figures 4, S4; Table S2). As a result, accuracy only

stands to benefit from incorporating partial sweeps into training since ignoring such

information leads to unacceptably high false negative rates of partial sweeps being called

neutral or linked.

*Figure 4. Confusion matrix heatmap of simulation experiment with partial sweeps*
*ignored during training. Given the BFS population history.*

## *partialS/HIC* binary classification outperforms a competing individual summary statistic approach

**Figure 5. ROC curves for binary classification of selective sweeps versus regions neutrally evolving or under linked selection.** *Given the BFS population history.*

To assess whether our deep learning method extends inferential resolution beyond the signal conferred by *iHS*, a statistic explicitly designed for detecting partial sweeps [30], we compared receiver operating characteristic (ROC) curves for the binary classification task of broadly detecting selective sweeps (*i.e.* any of the four selection states involving a sweep within the focal sub-window) vs. neutral regions or linked sweeps (Figure 1). Producing a ROC curve, which plots true positive against false positive rates given varying thresholds, for *partialS/HIC* per population required optimizing a separate CNN, keeping the same whole training dataset as well as architecture of network layers (Figure 2) except with two

final output responses (*i.e.* sweep in central sub-window vs. no sweep in central sub-

window) instead of nine. Mean, maximum, and proportion of outlier *iHS* values across SNPs

within the central sub-window of the training simulations were used to obtain three more

respective ROC curves for each population history. All sub-window variants of the *iHS*

statistic performed quite poorly (median AUC for: $E[iHS]$ = 0.555; maximum *iHS* = 0.505),

especially in contrast to the *partialS/HIC* binary classifier (median AUC = 0.939), in

identifying selective sweeps to the focal sub-window (Figures 5, S5).

## Soft and partial sweeps are commonplace among *A. gambiae* populations

294 *Figure 6. Genome-wide sweep calls across empirical mosquito population datasets.*

295 Turning our attention to the Ag1000G phase I data, we applied our nine-state CNNs to the

296 corresponding *A. gambiae* population datasets, classifying 5 KB segments using a 55 KB full

sliding window throughout the whole genome (Figure 1). Each of the eight mosquito populations contains a large number of sub-windows identified as completed soft sweeps (median fraction of total calls genome-wide = 5.01%) as well as partial sweeps (median fraction of total calls genome-wide for partial hard sweep = 2.84%; median fraction of total calls genome-wide for partial soft sweep = 7.24%), coupled with only a handful of completed hard sweep predictions (median fraction of total calls genome-wide = 0.03%) (Figure 6; Table S3). Partial soft sweeps were typically discovered the most often (median proportion of sweep calls = 52.59%), with completed soft sweeps often following (median proportion of sweep calls = 28.80%) and partial hard sweeps usually being the third most numerous class of detected sweep (median proportion of sweep calls = 19.75%). Notably, our estimated false discovery rates (FDRs) are higher for soft sweeps (median FDR for completed soft sweeps = 11.09%; median FDR for partial soft sweeps = 12.20%) compared to hard sweeps (median FDR for completed hard sweeps = 0.00%; median FDR for partial hard sweeps = 0.39%); this implies that individual soft sweep candidates should be viewed with more caution, though we should be able to estimate the genome-wide proportion of these classes well. After false discovery correction, classifications for partial soft sweeps still outnumber those for completed soft sweeps in AOM, BFS, CMS, and UGS, as well as for partial hard sweeps in all populations but GNS. Importantly, had partial sweeps not been accounted for in the training process, our results suggest that we would have both underestimated the total number of sweeps and incorrectly labeled many of our partial sweeps (Figures 4, S4). This would have led to the conclusion that adaptation from standing variation rather than *de novo* mutations dominate selective sweep dynamics in these *A. gambiae* populations. While it is clear that soft sweeps are indeed more common in these data, our results suggest that hard sweeps often occur as well, though with few reaching fixation. Furthermore, the *partialS/HIC* classifications indicate that most selective sweeps in these population samples are incomplete, suggesting that we are capturing a view of selection in progress.

## Selective sweeps are significantly enriched in functional regions of the *A. gambiae* genome

To elucidate broad characteristics underlying the genomic targets of selection, we used permutation tests of sweep call locations to discover enrichment patterns in the following DNA regions of interest: gene, mRNA, exon, CDS, five-prime UTR, and three-prime UTR (Figure 1). Permutation tests were based on the total number of calls for the four selection states with sweeps occurring within the focal sub-window, as well as the individual number of calls for each of these states respectively. Across all eight population datasets and for all six DNA regions under investigation, there is a statistically significant enrichment of total sweep calls along with completed soft sweeps calls in particular, whereas completed hard sweep calls are not significantly enriched in any single case (Figures 7, S6; Table S4). Conversely, partial sweep enrichment varies among populations as well as individual DNA regions. Specifically, partial hard sweeps are significantly enriched in five of the six DNA regions for BFS and CMS, and four of the DNA regions for UGS; while partial soft sweeps are significantly enriched in all six DNA regions for UGS, five of the DNA regions for BFM, and four of the DNA regions for BFS.

**Figure 7. Enrichments of selective sweeps within DNA regions.** *Statistically significant (p < 0.05) enrichments in green.*

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## Insecticide resistance loci, especially related to metabolism, are significantly enriched for selective sweeps

We performed a similar permutation analysis for four sets of genes known to confer insecticide resistance (IR) (Figure 1), finding at least one set of IR genes to be statistically significant for every population dataset in enrichment of total sweep calls (*i.e.* aggregate of all four sweep classes) and completed soft sweeps, respectively (Figures 8, S7; Table S5). In particular, metabolism-related IR genes are significantly enriched for each of these cases. Furthermore, IR genes corresponding to well-characterized resistance loci (*i.e.* target sites) are significantly enriched for AOM and BFM total sweep calls as well as completed soft sweeps in AOM, BFM, and GNS; IR genes associated with behavior are significantly enriched for BFM and GNS total sweep calls as well as completed soft sweeps in AOM, CMS, and GAS; and IR genes affiliated with cuticular activity are significantly enriched for completed soft sweeps in GWA and UGS. In contrast, completed hard sweeps are only significantly enriched in BFS, GNS, GWA, and UGS for IR genes connected to behavior (as well as metabolism for BFS). For partial sweeps, significant enrichment only occurs within BFM (partial soft sweeps in metabolism as well as behavior IR genes), CMS (partial hard sweeps in metabolism as well as target site IR genes), and UGS (partial hard sweeps in metabolism IR genes).

## Completed soft sweeps are significantly enriched within the same GO term annotations across populations

To uncover further functional traits targeted by selection, we used our permuted datasets to ask for which individual gene ontology (GO) terms our sweep candidates are enriched (Figure 1). Only completed soft sweeps, as well as the total of all four sweep states in combination, are significantly enriched for any GO terms, except for two single cellular components GO terms in UGS ("membrane" is enriched for completed hard sweeps and "nuclear cohesion complex" is enriched for partial hard sweeps); partial soft sweeps are therefore not significantly enriched for any GO terms among populations (Table S6). For

the completed soft sweep significant enrichments, we found six cases of the same GO term

in all eight populations. Three of these belong to the cellular components GO domain

("nucleus", "membrane" and "integral component of membrane"), and the other three are

connected to molecular function, specifically binding ("nucleic acid binding", "protein

binding" and "ATP binding"). All six of these terms, especially those conferring binding

function, are also enriched for total sweep calls across multiple datasets: "nucleic acid

binding" and "ATP binding" in seven populations; "protein binding" and "nucleus" in six

populations; "integral component of membrane" in five populations; and "membrane" in

three populations, one of which is significantly enriched for this GO term of completed hard

sweeps as well, the single example of such among all populations. Other cases involving the

same GO term significantly enriched for completed soft sweeps in over half of the

populations include: "binding", "cytoplasm", and "zinc ion binding" in seven populations;

"RNA binding" in six populations; and "mRNA splicing, via spliceosome" and "ATPase

activity" in five populations.

**Figure 8. Enrichments of selective sweeps within groupings of insecticide resistance genes.** *Statistically significant (p < 0.05) enrichments in green.*

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# Discussion

## *partialS/HIC* elucidates both species-wide and population-specific sweep dynamics within *A. gambiae*

The Ag1000G data provided the opportunity to investigate selection at both the continental scale, where wide-reaching impact across the whole species complex could be uncovered, and the regional level, revealing population-specific sweep dynamics. For the former, we observed that *A. gambiae* populations consistently experienced very few completed hard sweeps, with nearly all sweeps being partial and/or soft. In fact, the impact of completed hard sweeps on the adaptive process within mosquitos appears to be even more limited than what was observed previously in humans [33]. This is likely a result of the much larger population sizes and concordant levels of genetic variation that are maintained within *Anopheles* populations. Importantly, we find a large number of ongoing selective sweeps within these populations, particularly in comparison to the number of completed sweeps. There are multiple reasons why this might be the case. A trivial explanation may simply be that we only have power to detect sweeps that have completed in the past few hundred generations, though this seems unlikely. More plausibly, a large number of ongoing sweeps might be expected given the recent change in environment induced by vector control efforts. Another possible explanation is that the frequency dynamics of beneficial alleles within a population is often more complex than assumed and may indeed contain an overdominant component [34]. This would mean that some portion of the partial sweeps that we are observing in *Anopheles* is actually balanced, or transiently balanced, polymorphisms. A fourth class of explanation is that beneficial mutations may not be able to fix in populations due to competition with beneficial mutations on other genes that have originated in different parts of the species range [35]. Indeed, each of these factors may play some role in our reported abundance of partial sweeps.

Although such genome-wide sweep patterns occur species-wide, enrichment behavior seems much more population-specific. For instance, while every population possesses significant enrichment of completed soft sweeps coupled with no completed hard sweep significant enrichments for the six functional DNA regions studied here, partial

sweep enrichments vary widely among datasets. Sweep behavior is even more
idiosyncratic for insecticide resistance genes, as the only constant between populations is
that metabolism is a recurring target of selection, especially for completed soft sweeps.

These findings from the Ag1000G data provide important genomic resources that
will inform continental-wide strategies that apply to the entire *A. gambiae* species complex,
as well as aid management efforts in specializing to certain populations and localities,
which can improve malaria control efficacy. Such insight into mosquito vector evolution
may also help curb future insecticide resistance adaptation, and in turn prevent impending
crises of vector control failure. However, it is important to consider that our partial sweep
calls could be capturing more complex selective dynamics at play, for example polygenic
and quantitative trait adaptation [36,37], balancing selection [38], and introgression of
beneficial alleles. These could lead to different modes of adaptation for the same genomic
region across populations, for instance a favorable SNP undergoing a soft sweep at its
origin and then carried to neighboring populations (as was suggested in Miles *et al.* [6])
may appear to be experiencing a partial hard sweep in those recipient populations. Such
complicated interactions merit further investigation on the Ag1000G data, which would not
only continue advancing methodological development for population genetics, but also
address interesting questions for a widespread and ecologically important organism that
has crucial ramifications on wildlife management and public health.

## *partialS/HIC* offers powerful and unprecedented detection of partial sweeps

Supervised machine learning approaches are rapidly gaining traction among population
geneticists, with deep learning in particular beginning to experience increased attention
and methodological development due to its exciting potential to unlock classic population
genetics problems. Examples of successful SML implementation in population genomics
include demographic model choice [39], demographic parameter inference [40],
comparative analysis of independent single-population size changes [41], identification of

introgressed regions [42], recombination rate estimation [43–45], and genomic scans of
selective sweeps [24]; deep learning specifically has been employed for joint inference of
demography and selection [25], discovery of recombination hotspots [46], estimation of
demographic and recombination parameters [47], discovery of functional variants [48],
and differentiating between hard and soft sweeps from neutral regions [26]. These
applications especially benefit from the ability to handle high dimensional input data and
bypassing the need of a likelihood function, which is due to SML uncovering data patterns
from leveraging *a priori* information through a training algorithm [25,28]. CNNs expand
this utility to image processing, which has been demonstrated with *diploS/HIC* to be a
powerful tool for exploiting the genomic spatial distribution of multiple population-level
summary statistics to detect selective sweeps [26].

Here, we demonstrated with *partialS/HIC* that deep learning can be extended to
partial sweeps, especially partial hard sweeps, yielding greater accuracy and robustness
than has been previously attained. We also showcased consistent performance in the face
of several underlying demographic backgrounds. Specifically, *partialS/HIC* achieves
dependable discovery of selective sweeps, excellent simultaneous disambiguation between
partial and completed sweeps as well as between hard and soft sweeps, and reliable spatial
localization of selection targets in the genome. Moreover, we have shown that partial
sweeps remain mostly undetected if ignored from the training process, even though such
selection may be commonplace throughout a genome as with the Ag1000G data. As a result,
many previous studies scanning for either complete or ongoing selective sweeps solely (*i.e.*
not jointly inferring both types of selection) may have overlooked an important subset of
evolutionary events [35]. Researchers may then be interested in reexamining datasets with
*partialS/HIC* to elucidate the relative contributions of fixed versus incomplete sweeps to
adaptive evolution.

Importantly, the efficacy of *partialS/HIC* relies on several factors that are
unexplored here, including simulation prior specifications, CNN architecture with respect
to construction and parameterization of neural network layers, and data structure. Hence,
it is prudent for future implementations to validate performance by testing a range of
configurations, given a project's individual intricacies, to assess robustness and inherent

assumptions. In particular, future exploration of alternate image constructions could be

potentially of great methodological benefit. Such images could be derived from different

ordering schemes and/or suites of summary statistics, as well as without summary

statistics entirely, instead directly exploiting sequence alignments [46,47] or even raw

reads. More broadly, CNNs can be further extended to address other long-standing efforts

in evolutionary biology, such as parameter inference under complex isolation-migration

models or phylogenetic reconstruction.

# Methods

## Simulations for training and testing CNN classifier

We used *discoal* [31] to simulate training and test datasets corresponding to each *A.*

*gambiae* population under nine different selection states: neutrally evolving, completed

hard sweep, completed soft sweep, partial hard sweep, partial soft sweep, and linked

region for every one of the four sweep classes (Figure 1; Table S7). For the four sweep

types, the target SNP was located in the exact middle position within the central, or sixth in

sequence, sub-window of 11 in total; the selected SNP was placed in the middle within one

of the other ten sub-windows for linked sweeps. There were 2,000 training examples per

selection state (with selected sub-window randomized for linked sweeps) and 1,000 test

examples per class (including for each of the ten linked sweep locations), resulting in a

training dataset of 18,000 simulations and a test dataset of 45,000 simulations given each

demographic history, thus totaling 144,000 training and 360,000 test simulations. To

conduct single-population simulations with *discoal*, we used the *stairway plot* [53] point

estimates from Miles *et al.* [6] for size change parameters as well as $N_0$ (present-day

effective population size), assumed a mutation rate ($\mu$) of $3.5 \times 10^{-9}$ mutations per base pair

per generation, and performed random draws for locus-wide mutation and recombination

rates from the following distributions for each independent replicate: $\theta \sim U(\frac{2 \times E[\theta]}{11.0}, \frac{2 \times E[\theta]}{1.1})$,

where $E[\theta] = 4N_0\mu L$ and $L$ is the length of the simulated sequence with $L = 55{,}000$ base

pairs; $\rho \sim TEXP(2 \times E[\theta], 6 \times E[\theta])$, where $\rho = 4N_0 r L$, $r$ is the recombination rate per base

pair, and *TEXP*($\beta$, maximum value) is a truncated exponential distribution with mean $\beta$; $s \sim$

$U(1.0 \times 10^{-4}, 1.0 \times 10^{-2})$; end time of sweep $\sim U(0, 2,000)$ generations ago, which represents

fixation for completed sweeps and the transition back to neutral evolution for partial

sweeps; selected SNP allele frequency at onset of soft sweep $\sim U(\frac{1}{N_0}, 0.2)$; and selected SNP

allele frequency at end of partial sweep $\sim U(0.20, 0.99)$.

## Constructing two-dimensional feature vector images of summary statistics

The eight training and test datasets, as well as empirical datasets, were converted into two-

dimensional feature vector matrices for downstream deep learning (Figure 1); this was

performed within the Python environment and required usage of the module *numpy*. Prior

to this two-dimensional transformation, the simulated data were modified to better

account for uncertainty within the empirical data, specifically: 1) sites that were missing

any individual calls or could not be polarized against the outgroup were excluded; and 2)

incorrect identification of the derived allele. For the former, each simulation randomly

drew from a distribution of 1,552 masking profiles (with test simulations drawing without

replacement per selection class of 1,000 simulations), which determined the exact sites to

be omitted from further analysis; a masking profile consisted of the site positions within a

single full 55 KB window on the *A. gambiae* genome that had absent at least one sample

throughout the entirety of the Ag1000G data and/or ancestral state information, and the

total set represented all 1,552 sequential, non-overlapping windows (*e.g.* 2L: 1–55,000; 2L:

55,001–110,000; 2L: 110,001–165,000; etc.) where the proportion of masked sites did not

exceed 75% in any of the constituent sub-windows (*i.e.* 1,250 sites). To account for

mispolarization, estimated rates were obtained from Miles *et al.* [6] and exploited via a

binomial distribution to mispolarize a random subset of SNPs to the other allele per

simulation.

The empirical data similarly underwent processing for compatibility with the

simulated data. First, chromosomes were delineated into sequential 5 KB sub-windows

(*e.g.* positions 1-5,000 formed the first sub-window, positions 5,001-10,000 formed the
second sub-window, etc.), with the aforementioned masking criteria applied across sites
and remaining SNPs polarized. Within each population dataset, all polymorphic positions
containing more than two alleles were further removed from analysis, such that only
polarized monomorphic and biallelic sites comprising a full data matrix of no missing data
were left. Sub-windows containing no SNPs or less than 25% of the original sites were
subsequently discarded, and every configuration of 11 contiguous 5 KB sub-windows of
those remaining formed a single full window, which would be classified into one of the nine
selection states based upon its central sub-window while using spatial information from
the neighboring five sub-windows on either side. To clarify, this eliminated any window
that did not contain a consecutive sequence of 11 sub-windows that survived data filtering,
and resulted in a sliding window that progressed a single sub-window at a time, such that
succeeding full windows could be overlapping by up to ten sub-windows.

Every independent simulation totaling 55 KB in length from 11 sub-windows of 5
KB, as well as empirical sequence of 11 adjacent sub-windows per population, was then
transformed into 89 separate summary statistic vectors, each with 11 elements that
captured population-level variation across the sampled individuals per sub-window. The
first 17 summary statistics, which were $\pi$ [54], $\theta_W$ [55], Tajima's $D$ [14], $\theta_H$ [15], Fay-Wu's $H$
[15], number of haplotypes, $H_1$ [52], $H_{12}$ [52], $H_2/H_1$ [52], $Z_{nS}$ [56], $\omega$ [16], $E[iHS]$ [30],
maximum *iHS* [30], proportion of outlier *iHS* values [30], variance of pairwise genotype
distances [26], skewness of pairwise genotype distances [26], and kurtosis of pairwise
genotype distances [26], were calculated with the Python package *scikit-allel* as done with
*diploS/HIC* [26]. Values for *iHS* were standardized within 50 derived allele frequency bins,
following mispolarization in the case of simulated data. Outlier *iHS* values were defined as
within either 2.0% tail of the distribution obtained from simulations of neutral evolution
under the appropriate demographic history.

The remaining 72 summary statistics originated from SAFE, a recently developed
statistic [32], and its various components; these SAFE-derived statistics included
summaries for the distribution of values for: haplotype allele frequency (HAF), which is the
sum of derived allele counts across all the derived alleles present within a sequence;

unique HAF score (*i.e.* each unique HAF value is counted only once, even if representing
multiple individuals); $\varphi$, which is the sum of HAF scores for sequences harboring the
derived allele, divided by the total sum of HAF scores across all sequences; $\kappa$, which is the
proportion of distinct HAF scores that carry the derived allele; derived allele frequency;
and SAFE itself, which is the difference between $\varphi$ and $\kappa$ normalized against the derived
allele frequency. Notably, HAF is calculated per sequence, whereas $\varphi$, $\kappa$, derived allele
frequency, and SAFE are calculated per polymorphism. The following distribution
summaries were utilized to construct individual values spanning a sub-window: mean,
median, mode; 2.5%, 25%, 75%, and 97.5% quartiles; maximum, variance, standard
deviation, skewness, and kurtosis. Importantly, each summary statistic vector was
normalized, in the same manner as the preceding versions to *partialS/HIC* [24,26], to
capture signal solely from the relative spatial distribution of the summary statistics across
the 11 sub-windows, rather than allowing influence from absolute values. Subsequently,
the 89 vectors were vertically collated to form a two-dimensional matrix that could then be
exploited for image processing. The arrangement of these vectors were such that the 11
columns corresponded to the series of sub-windows from left to right, and the 89 rows of
summary statistics were in the order presented here (with the distribution summaries
iterating first for every SAFE component, *e.g.* row 52: skewness of $\varphi$ values; row 53:
kurtosis of $\varphi$ values; row 54: $E[\kappa]$). Importantly, column and row order affects deep
learning optimization, which may have consequences on overall efficacy, due to the
convolutional and pooling windows employed by the CNN architecture, hence related
summary statistics were grouped together (*e.g.* alternative distribution summaries of a
SNP-based statistic, various SAFE derivatives). Heatmap images, based on median values
per statistic and sub-window, were generated in R for the neutral case and each of the four
sweep states under every population history from the training simulations.

## Training and testing CNNs for deep learning implementation

591 The architecture of our CNN was composed of the following sequential layers: 1) 2D
592 convolutional layer with 256 filters using 3×6 windows and "same" padding; 2) 2D max

pooling layer given a 3×3 window; 3) a second 2D convolutional layer of 256 filters based on 3×3 windows, "same" padding, and ReLU activation; 4) a second 2D max pooling layer also with a 3×3 window; 5) dropout layer with p=0.25; 6) flattening layer; 7) fully-connected layer with ReLU activation to 512 responses; 8) a second dropout layer with p=0.50; 9) a second fully-connected layer with ReLU activation to 128 elements; 10) another dropout layer with p=0.50; and 11) softmax activation layer to 9 states (Figures 1–2). This architecture was trained using the Python module *Keras* [57] given the *Adam* optimizer [58], with 20 epochs, batch size of 32 simulations per step within an epoch, and 10% of the training data (*e.g.* 1800 simulations from the total nine-state training dataset) randomly removed as a validation set during optimization. Training was performed for every population demography under three experimental settings: 1) given the full set of training data distributed across nine selection states; 2) exploiting a subset of the training data from only five of the selection states, specifically those involving neutral regions or completed sweeps; 3) deploying the entire training data, but with binary classification between selective sweeps in the focal sub-window and all unselected classes (*i.e.* neutral class together with every linked class). The same test datasets were used for the first two simulation experiments, producing overall accuracy measures as well as confusion matrix heatmaps to assess misclassification bias for each of 45 classes, in this case treating different sub-window placements of linked sweeps discretely. Moreover, to explore the effect of demographic misspecification, we conducted a single additional test under the first experimental set-up whereby the CNN trained on the GAS simulations was applied to the CMS test simulations. Regarding the binary classification experiment, the Python module *sklearn*, which is available at http://scikit-learn.org/stable/ [59], was used for building ROC curves to evaluate accuracy and sensitivity. For comparison, ROC curves were also constructed from the training simulations based on the focal sub-window mean *iHS*, maximum *iHS*, and proportion of *iHS* values that were outliers, respectively.

## Detecting selective sweeps for *A. gambiae* population datasets

To scan the genome for signatures of selective sweeps, the nine-state trained CNNs were
applied to the eight empirical mosquito datasets, with the underlying simulated
demography matched to the sampled population (Figure 1). Calls were corrected for false
discovery by exploiting the accuracy and error rates for neutral regions from the nine-state
simulation experiment, such that the amount of neutral calls was assumed to be
underestimated while the amount of calls for the remaining eight selection states were
assumed to be inflated. Subsequently, we produced sets of 10,000 randomly permuted calls
across the genome to derive null expectations of sweep enrichment, following Schrider and
Kern [33]. Using the gene annotation file "Anopheles-gambiae-
PEST_BASEFEATURES_AgamP4.7.gff3.gz" from VectorBase, we exploited these permuted
datasets to assess statistically significant enrichment within certain DNA regions,
groupings of known IR genes (N. Harding, *pers. comm.*), and all basic GO term definitions
from http://www.geneontology.org (last accessed February 18, 2015). The DNA regions of
interest included gene, mRNA, exon, CDS, five-prime UTR, and three-prime UTR; IR genes
were assigned to four functional categories: metabolism, target sites, behavior, and
cuticular. To determine significant enrichment, the number of inferred calls for a particular
DNA region or IR gene category had to have a *p*-value < 0.05 based on the respective
distribution of 10,000 permutations; for the GO terms, we deployed a corrected *q*-value <
0.05 due to concerns of false discovery stemming from the large number of terms tested for
enrichment.

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                                 **Figure Captions**

**Figure 1. Flowchart of methodological procedure.** Major steps highlighted in green. Note that processing of simulated data incorporated uncertainties within the empirical data, specifically with respect to masking sites from calculation of summary statistics.

**Figure 2. CNN architecture of neural network layers.** The input feature vector image is passed to a 2D convolutional layer with 256 filters using a 3×6 receptive field. Next is a 2D max pooling layer given a 3×3 receptive field. Then there is a second 2D convolutional layer of 256 filters based on a 3×3 receptive field and ReLU activation. Afterward is a second 2D max pooling layer, also with a 3×3 receptive field. The tensor is then flattened and passed to two fully-connected layers with ReLU activation, resulting in 512 and 128 nodes respectively. Finally, a softmax activation layer classifies the 9 responses.

**Figure 3. Confusion matrix heatmap of simulation experiment including partial sweep training.** Given the BFS population history.

**Figure 4. Confusion matrix heatmap of simulation experiment with partial sweeps ignored during training.** Given the BFS population history.

**Figure 5. ROC curves for binary classification of selective sweeps versus regions neutrally evolving or under linked selection.** Given the BFS population history.

**Figure 6. Genome-wide sweep calls across empirical mosquito population datasets.**

**Figure 7. Enrichments of selective sweeps within DNA regions.** Statistically significant ($p < 0.05$) enrichments in green.

**Figure 8. Enrichments of selective sweeps within groupings of insecticide resistance genes.** Statistically significant ($p < 0.05$) enrichments in green.

**Figure S1. Feature vector heatmaps for neutral and four sweep states under each population history.** Heatmaps derived from median values of a single training dataset, each assuming a different population history. Note focal sub-window for four sweep states versus neutral state across populations.

**Figure S2. Confusion matrix heatmaps of simulation experiment including partial sweep training under each population history.**

**Figure S3. Confusion matrix heatmap of demographic misspecification test.** Training on simulations (including partial sweeps) given the GAS population history while testing on simulations given the CMS population history.

**Figure S4. Confusion matrix heatmaps of simulation experiment with partial sweeps ignored during training under each population history.**

**Figure S5. ROC curves for binary classification of selective sweeps versus regions neutrally evolving or under linked selection for each population history.**

**Figure S6. Enrichments of selective sweeps within DNA regions for each empirical mosquito population dataset.** Statistically significant ($p < 0.05$) enrichments in green.

**Figure S7. Enrichments of selective sweeps within groupings of insecticide resistance genes for each empirical mosquito population dataset.** Statistically significant ($p < 0.05$) enrichments in green.

**Table S1.** Accuracy rate for deep learning *in silico* test per simulated population dataset.

| Population | Accuracy |
|---|---|
| AOM | 0.610 |
| BFM | 0.661 |
| BFS | 0.691 |
| CMS | 0.711 |
| GAS | 0.667 |
| GNS | 0.546 |
| GWA | 0.625 |
| UGS | 0.678 |
| *median* | 0.664 |
| *mean* | 0.648 |

**Table S2.** Accuracy rate for five-state deep learning *in silico* test per simulated population dataset (neutral regions and completed sweeps only).

| Population | Accuracy |
|---|---|
| AOM | 0.822 |
| BFM | 0.872 |
| BFS | 0.881 |
| CMS | 0.897 |
| GAS | 0.830 |
| GNS | 0.792 |
| GWA | 0.780 |
| UGS | 0.906 |
| *median* | 0.851 |
| *mean* | 0.848 |

**Table S3.** Nine-state calls for individual chromosome arms and genome-wide for each empirical mosquito population dataset.

| | AOM | BFM | BFS | CMS | GAS | GNS | GWA | UGS | *median* | *mean* |
|---|---|---|---|---|---|---|---|---|---|---|
| | *neutral (proportion)* | | | | | | | | | |
| **2L** | 0.4524 | 0.6649 | 0.2929 | 0.0167 | 0.3153 | 0.2960 | 0.0395 | 0.1990 | 0.2944 | 0.2846 |
| **2R** | 0.4217 | 0.3822 | 0.2899 | 0.0046 | 0.2227 | 0.3465 | 0.0335 | 0.2231 | 0.2565 | 0.2405 |
| **3L** | 0.5452 | 0.6728 | 0.4012 | 0.0067 | 0.2709 | 0.5540 | 0.3315 | 0.3663 | 0.3838 | 0.3936 |
| **3R** | 0.5181 | 0.6202 | 0.3123 | 0.0069 | 0.2676 | 0.4124 | 0.2433 | 0.3327 | 0.3225 | 0.3392 |
| genome-wide | 0.4767 | 0.5608 | 0.3172 | 0.0081 | 0.2626 | 0.3912 | 0.1483 | 0.2761 | 0.2967 | 0.3051 |
| | *completed hard (proportion)* | | | | | | | | | |
| **2L** | 0.0000 | 0.0000 | 0.0000 | 0.0006 | 0.0004 | 0.0000 | 0.0000 | 0.0004 | 0.0000 | 0.0002 |
| **2R** | 0.0010 | 0.0004 | 0.0002 | 0.0000 | 0.0002 | 0.0002 | 0.0009 | 0.0002 | 0.0002 | 0.0004 |
| **3L** | 0.0000 | 0.0004 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0008 | 0.0000 | 0.0000 | 0.0002 |
| **3R** | 0.0000 | 0.0008 | 0.0005 | 0.0000 | 0.0005 | 0.0003 | 0.0003 | 0.0007 | 0.0004 | 0.0004 |
| genome-wide | 0.0003 | 0.0004 | 0.0002 | 0.0001 | 0.0003 | 0.0002 | 0.0005 | 0.0004 | 0.0003 | 0.0003 |
| | *completed hard – linked (proportion)* | | | | | | | | | |
| **2L** | 0.0004 | 0.0004 | 0.0017 | 0.0035 | 0.0000 | 0.0019 | 0.0000 | 0.0007 | 0.0006 | 0.0011 |
| **2R** | 0.0045 | 0.0018 | 0.0013 | 0.0034 | 0.0016 | 0.0009 | 0.0018 | 0.0024 | 0.0018 | 0.0022 |
| **3L** | 0.0010 | 0.0020 | 0.0004 | 0.0027 | 0.0005 | 0.0013 | 0.0004 | 0.0008 | 0.0009 | 0.0011 |
| **3R** | 0.0028 | 0.0025 | 0.0020 | 0.0007 | 0.0003 | 0.0000 | 0.0000 | 0.0012 | 0.0009 | 0.0012 |
| genome-wide | 0.0026 | 0.0017 | 0.0014 | 0.0025 | 0.0007 | 0.0009 | 0.0007 | 0.0014 | 0.0014 | 0.0015 |
| | *completed soft (proportion)* | | | | | | | | | |
| **2L** | 0.0587 | 0.0309 | 0.0187 | 0.0273 | 0.0393 | 0.0596 | 0.0665 | 0.0540 | 0.0466 | 0.0444 |
| **2R** | 0.0763 | 0.0307 | 0.0254 | 0.0259 | 0.0664 | 0.0580 | 0.0817 | 0.0647 | 0.0614 | 0.0536 |
| **3L** | 0.0558 | 0.0242 | 0.0234 | 0.0403 | 0.0332 | 0.0511 | 0.0676 | 0.0547 | 0.0457 | 0.0438 |
| **3R** | 0.0446 | 0.0257 | 0.0168 | 0.0329 | 0.0304 | 0.0520 | 0.0716 | 0.0522 | 0.0388 | 0.0408 |
| genome-wide | 0.0601 | 0.0281 | 0.0212 | 0.0310 | 0.0449 | 0.0554 | 0.0732 | 0.0571 | 0.0501 | 0.0464 |
| | *completed soft – linked (proportion)* | | | | | | | | | |
| **2L** | 0.1106 | 0.0872 | 0.1333 | 0.2428 | 0.1537 | 0.3515 | 0.3744 | 0.2050 | 0.1793 | 0.2073 |
| **2R** | 0.1267 | 0.1635 | 0.1310 | 0.2699 | 0.2286 | 0.2983 | 0.4573 | 0.1666 | 0.1976 | 0.2302 |
| **3L** | 0.0837 | 0.0890 | 0.1257 | 0.3544 | 0.1034 | 0.2003 | 0.2353 | 0.1480 | 0.1368 | 0.1675 |
| **3R** | 0.0823 | 0.0920 | 0.1310 | 0.3211 | 0.0783 | 0.2407 | 0.2631 | 0.1572 | 0.1441 | 0.1707 |
| genome-wide | 0.1033 | 0.1139 | 0.1305 | 0.2955 | 0.1487 | 0.2755 | 0.3448 | 0.1682 | 0.1584 | 0.1975 |
| | *partial hard (proportion)* | | | | | | | | | |
| **2L** | 0.0281 | 0.0103 | 0.0463 | 0.0331 | 0.1380 | 0.0331 | 0.0395 | 0.0427 | 0.0363 | 0.0464 |
| **2R** | 0.0363 | 0.0241 | 0.0554 | 0.0836 | 0.0917 | 0.0359 | 0.0276 | 0.0293 | 0.0361 | 0.0480 |
| **3L** | 0.0168 | 0.0071 | 0.0138 | 0.0113 | 0.1624 | 0.0074 | 0.0118 | 0.0119 | 0.0118 | 0.0303 |
| **3R** | 0.0237 | 0.0135 | 0.0388 | 0.0176 | 0.1676 | 0.0315 | 0.0193 | 0.0113 | 0.0215 | 0.0404 |
| genome-wide | 0.0277 | 0.0151 | 0.0412 | 0.0405 | 0.1350 | 0.0291 | 0.0248 | 0.0236 | 0.0284 | 0.0422 |
| | *partial hard – linked (proportion)* | | | | | | | | | |
| **2L** | 0.0768 | 0.0223 | 0.1382 | 0.0864 | 0.1325 | 0.0581 | 0.0512 | 0.0823 | 0.0796 | 0.0810 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **2R** | 0.1011 | 0.0767 | 0.1338 | 0.1535 | 0.1334 | 0.0882 | 0.0372 | 0.0533 | 0.0947 | 0.0971 |
| **3L** | 0.0635 | 0.0115 | 0.0461 | 0.0329 | 0.1867 | 0.0234 | 0.0248 | 0.0184 | 0.0289 | 0.0509 |
| **3R** | 0.0811 | 0.0353 | 0.1112 | 0.0652 | 0.1821 | 0.0746 | 0.0341 | 0.0204 | 0.0699 | 0.0755 |
| **genome-wide** | 0.0841 | 0.0419 | 0.1122 | 0.0914 | 0.1564 | 0.0670 | 0.0370 | 0.0433 | 0.0755 | 0.0791 |
| *partial soft* (proportion) | | | | | | | | | | |
| **2L** | 0.0885 | 0.0475 | 0.0598 | 0.1040 | 0.0531 | 0.0510 | 0.1170 | 0.1146 | 0.0741 | 0.0794 |
| **2R** | 0.0708 | 0.0504 | 0.0737 | 0.0535 | 0.0499 | 0.0426 | 0.1024 | 0.1292 | 0.0621 | 0.0716 |
| **3L** | 0.0659 | 0.0461 | 0.0734 | 0.0839 | 0.0538 | 0.0438 | 0.1105 | 0.1296 | 0.0696 | 0.0759 |
| **3R** | 0.0761 | 0.0473 | 0.0702 | 0.1547 | 0.0545 | 0.0426 | 0.1249 | 0.1447 | 0.0732 | 0.0894 |
| **genome-wide** | 0.0751 | 0.0481 | 0.0698 | 0.0986 | 0.0526 | 0.0445 | 0.1133 | 0.1308 | 0.0724 | 0.0791 |
| *partial soft – linked* (proportion) | | | | | | | | | | |
| **2L** | 0.1846 | 0.1365 | 0.3092 | 0.4855 | 0.1678 | 0.1489 | 0.3119 | 0.3013 | 0.2429 | 0.2557 |
| **2R** | 0.1616 | 0.2704 | 0.2893 | 0.4055 | 0.2054 | 0.1293 | 0.2575 | 0.3312 | 0.2640 | 0.2563 |
| **3L** | 0.1683 | 0.1469 | 0.3159 | 0.4679 | 0.1891 | 0.1188 | 0.2172 | 0.2704 | 0.2031 | 0.2368 |
| **3R** | 0.1712 | 0.1629 | 0.3173 | 0.4010 | 0.2186 | 0.1459 | 0.2436 | 0.2795 | 0.2311 | 0.2425 |
| **genome-wide** | 0.1702 | 0.1898 | 0.3062 | 0.4322 | 0.1989 | 0.1362 | 0.2575 | 0.2991 | 0.2282 | 0.2487 |
| *neutral* (count) | | | | | | | | | | |
| **2L** | 1,125 | 1,875 | 848 | 52 | 802 | 795 | 108 | 568 | 798.5 | 771.6 |
| **2R** | 1,764 | 1,730 | 1,361 | 23 | 950 | 1,552 | 147 | 1,034 | 1,197.5 | 1,070.1 |
| **3L** | 1,134 | 1,694 | 1,044 | 20 | 579 | 1,278 | 789 | 958 | 1,001.0 | 937.0 |
| **3R** | 1,858 | 2,441 | 1,264 | 31 | 977 | 1,569 | 935 | 1,352 | 1,308.0 | 1,303.4 |
| **genome-wide** | 5,881 | 7,740 | 4,517 | 126 | 3,308 | 5,194 | 1,979 | 3,912 | 4,214.5 | 4,082.1 |
| *completed hard* (count) | | | | | | | | | | |
| **2L** | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 0.0 | 0.5 |
| **2R** | 4 | 2 | 1 | 0 | 1 | 1 | 4 | 1 | 1.0 | 1.8 |
| **3L** | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0.0 | 0.4 |
| **3R** | 0 | 3 | 2 | 0 | 2 | 1 | 1 | 3 | 1.5 | 1.5 |
| **genome-wide** | 4 | 6 | 3 | 2 | 4 | 2 | 7 | 5 | 4.0 | 4.1 |
| *completed hard – linked* (count) | | | | | | | | | | |
| **2L** | 1 | 1 | 5 | 11 | 0 | 5 | 0 | 2 | 1.5 | 3.1 |
| **2R** | 19 | 8 | 6 | 17 | 7 | 4 | 8 | 11 | 8.0 | 10.0 |
| **3L** | 2 | 5 | 1 | 8 | 1 | 3 | 1 | 2 | 2.0 | 2.9 |
| **3R** | 10 | 10 | 8 | 3 | 1 | 0 | 0 | 5 | 4.0 | 4.6 |
| **genome-wide** | 32 | 24 | 20 | 39 | 9 | 12 | 9 | 20 | 20.0 | 20.6 |
| *completed soft* (count) | | | | | | | | | | |
| **2L** | 146 | 87 | 54 | 85 | 100 | 160 | 182 | 154 | 123.0 | 121.0 |
| **2R** | 319 | 139 | 119 | 129 | 283 | 260 | 358 | 300 | 271.5 | 238.4 |
| **3L** | 116 | 61 | 61 | 121 | 71 | 118 | 161 | 143 | 117.0 | 106.5 |
| **3R** | 160 | 101 | 68 | 148 | 111 | 198 | 275 | 212 | 154.0 | 159.1 |
| **genome-wide** | 741 | 388 | 302 | 483 | 565 | 736 | 976 | 809 | 650.5 | 625.0 |
| *completed soft – linked* (count) | | | | | | | | | | |
| **2L** | 275 | 246 | 386 | 756 | 391 | 944 | 1,024 | 585 | 488.0 | 575.9 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **2R** | 530 | 740 | 615 | 1,343 | 975 | 1,336 | 2,005 | 772 | 873.5 | 1,039.5 |
| **3L** | 174 | 224 | 327 | 1,065 | 221 | 462 | 560 | 387 | 357.0 | 427.5 |
| **3R** | 295 | 362 | 530 | 1,443 | 286 | 916 | 1,011 | 639 | 584.5 | 685.3 |
| genome-wide | 1,274 | 1,572 | 1,858 | 4,607 | 1,873 | 3,658 | 4,600 | 2,383 | 2,128.0 | 2,728.1 |
| | *partial hard* (count) | | | | | | | | | |
| **2L** | 70 | 29 | 134 | 103 | 351 | 89 | 108 | 122 | 105.5 | 125.8 |
| **2R** | 152 | 109 | 260 | 416 | 391 | 161 | 121 | 136 | 156.5 | 218.3 |
| **3L** | 35 | 18 | 36 | 34 | 347 | 17 | 28 | 31 | 32.5 | 68.3 |
| **3R** | 85 | 53 | 157 | 79 | 612 | 120 | 74 | 46 | 82.0 | 153.3 |
| genome-wide | 342 | 209 | 587 | 632 | 1,701 | 387 | 331 | 335 | 364.5 | 565.5 |
| | *partial hard – linked* (count) | | | | | | | | | |
| **2L** | 191 | 63 | 400 | 269 | 337 | 156 | 140 | 235 | 213.0 | 223.9 |
| **2R** | 423 | 347 | 628 | 764 | 569 | 395 | 163 | 247 | 409.0 | 442.0 |
| **3L** | 132 | 29 | 120 | 99 | 399 | 54 | 59 | 48 | 79.0 | 117.5 |
| **3R** | 291 | 139 | 450 | 293 | 665 | 284 | 131 | 83 | 287.5 | 292.0 |
| genome-wide | 1,037 | 578 | 1,598 | 1,425 | 1,970 | 889 | 493 | 613 | 963.0 | 1,075.4 |
| | *partial soft* (count) | | | | | | | | | |
| **2L** | 220 | 134 | 173 | 324 | 135 | 137 | 320 | 327 | 196.5 | 221.3 |
| **2R** | 296 | 228 | 346 | 266 | 213 | 191 | 449 | 599 | 281.0 | 323.5 |
| **3L** | 137 | 116 | 191 | 252 | 115 | 101 | 263 | 339 | 164.0 | 189.3 |
| **3R** | 273 | 186 | 284 | 695 | 199 | 162 | 480 | 588 | 278.5 | 358.4 |
| genome-wide | 926 | 664 | 994 | 1,537 | 662 | 591 | 1,512 | 1,853 | 960.0 | 1,092.4 |
| | *partial soft – linked* (count) | | | | | | | | | |
| **2L** | 459 | 385 | 895 | 1,512 | 427 | 400 | 853 | 860 | 656.0 | 723.9 |
| **2R** | 676 | 1,224 | 1,358 | 2,018 | 876 | 579 | 1,129 | 1,535 | 1,176.5 | 1,174.4 |
| **3L** | 350 | 370 | 822 | 1,406 | 404 | 274 | 517 | 707 | 460.5 | 606.3 |
| **3R** | 614 | 641 | 1,284 | 1,802 | 798 | 555 | 936 | 1,136 | 867.0 | 970.8 |
| genome-wide | 2,099 | 2,620 | 4,359 | 6,738 | 2,505 | 1,808 | 3,435 | 4,238 | 3,027.5 | 3,475.3 |
| | *neutral* (proportion) corrected for false discovery | | | | | | | | | |
| **2L** | 0.4922 | 0.7173 | 0.3247 | 0.0387 | 0.3700 | 0.3486 | 0.0502 | 0.2369 | 0.3367 | 0.3223 |
| **2R** | 0.4589 | 0.4122 | 0.3214 | 0.0107 | 0.2614 | 0.4081 | 0.0427 | 0.2656 | 0.2935 | 0.2726 |
| **3L** | 0.5932 | 0.7257 | 0.4448 | 0.0154 | 0.3180 | 0.6525 | 0.4218 | 0.4361 | 0.4405 | 0.4510 |
| **3R** | 0.5638 | 0.6690 | 0.3463 | 0.0160 | 0.3141 | 0.4857 | 0.3095 | 0.3960 | 0.3712 | 0.3876 |
| genome-wide | 0.5188 | 0.6050 | 0.3517 | 0.0188 | 0.3082 | 0.4608 | 0.1887 | 0.3287 | 0.3402 | 0.3476 |
| | *completed hard* (proportion) corrected for false discovery | | | | | | | | | |
| **2L** | 0.0000 | 0.0000 | 0.0000 | 0.0006 | 0.0004 | 0.0000 | 0.0000 | 0.0004 | 0.0000 | 0.0002 |
| **2R** | 0.0010 | 0.0004 | 0.0002 | 0.0000 | 0.0002 | 0.0002 | 0.0009 | 0.0002 | 0.0002 | 0.0004 |
| **3L** | 0.0000 | 0.0004 | 0.0000 | 0.0000 | 0.0000 | 0.0000 | 0.0008 | 0.0000 | 0.0000 | 0.0002 |
| **3R** | 0.0000 | 0.0008 | 0.0005 | 0.0000 | 0.0005 | 0.0003 | 0.0003 | 0.0007 | 0.0004 | 0.0004 |
| genome-wide | 0.0003 | 0.0004 | 0.0002 | 0.0001 | 0.0003 | 0.0002 | 0.0005 | 0.0004 | 0.0003 | 0.0003 |

| | completed hard – linked (proportion) corrected for false discovery | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| 2L | 0.0004 | -0.0011 | 0.0017 | 0.0035 | 0.0000 | 0.0019 | 0.0000 | 0.0007 | 0.0006 | 0.0009 |
| 2R | 0.0045 | 0.0009 | 0.0013 | 0.0034 | 0.0016 | 0.0009 | 0.0018 | 0.0024 | 0.0017 | 0.0021 |
| 3L | 0.0010 | 0.0005 | 0.0004 | 0.0027 | 0.0005 | 0.0013 | 0.0004 | 0.0008 | 0.0006 | 0.0009 |
| 3R | 0.0028 | 0.0012 | 0.0020 | 0.0007 | 0.0003 | 0.0000 | 0.0000 | 0.0012 | 0.0009 | 0.0010 |
| genome-wide | 0.0026 | 0.0005 | 0.0014 | 0.0025 | 0.0007 | 0.0009 | 0.0007 | 0.0014 | 0.0012 | 0.0013 |
| | completed soft (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.0498 | 0.0258 | 0.0177 | 0.0267 | 0.0345 | 0.0495 | 0.0652 | 0.0485 | 0.0415 | 0.0397 |
| 2R | 0.0680 | 0.0278 | 0.0244 | 0.0258 | 0.0630 | 0.0462 | 0.0805 | 0.0586 | 0.0524 | 0.0493 |
| 3L | 0.0451 | 0.0191 | 0.0221 | 0.0400 | 0.0291 | 0.0322 | 0.0563 | 0.0447 | 0.0361 | 0.0361 |
| 3R | 0.0345 | 0.0210 | 0.0158 | 0.0327 | 0.0263 | 0.0380 | 0.0632 | 0.0431 | 0.0336 | 0.0343 |
| genome-wide | 0.0507 | 0.0239 | 0.0202 | 0.0307 | 0.0408 | 0.0421 | 0.0681 | 0.0495 | 0.0415 | 0.0407 |
| | completed soft – linked (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.1012 | 0.0822 | 0.1304 | 0.2419 | 0.1463 | 0.3396 | 0.3727 | 0.2036 | 0.1749 | 0.2022 |
| 2R | 0.1180 | 0.1606 | 0.1281 | 0.2697 | 0.2234 | 0.2844 | 0.4559 | 0.1650 | 0.1942 | 0.2256 |
| 3L | 0.0724 | 0.0839 | 0.1217 | 0.3541 | 0.0971 | 0.1781 | 0.2214 | 0.1454 | 0.1335 | 0.1592 |
| 3R | 0.0716 | 0.0873 | 0.1278 | 0.3207 | 0.0721 | 0.2242 | 0.2529 | 0.1549 | 0.1414 | 0.1639 |
| genome-wide | 0.0934 | 0.1097 | 0.1273 | 0.2951 | 0.1425 | 0.2598 | 0.3385 | 0.1662 | 0.1544 | 0.1916 |
| | partial hard (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.0277 | 0.0103 | 0.0460 | 0.0330 | 0.1369 | 0.0331 | 0.0395 | 0.0425 | 0.0363 | 0.0461 |
| 2R | 0.0359 | 0.0241 | 0.0551 | 0.0836 | 0.0909 | 0.0359 | 0.0276 | 0.0291 | 0.0359 | 0.0478 |
| 3L | 0.0162 | 0.0071 | 0.0134 | 0.0113 | 0.1614 | 0.0074 | 0.0118 | 0.0114 | 0.0116 | 0.0300 |
| 3R | 0.0231 | 0.0135 | 0.0384 | 0.0175 | 0.1667 | 0.0315 | 0.0193 | 0.0109 | 0.0212 | 0.0401 |
| genome-wide | 0.0272 | 0.0151 | 0.0409 | 0.0405 | 0.1341 | 0.0291 | 0.0248 | 0.0233 | 0.0282 | 0.0419 |
| | partial hard – linked (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.0748 | 0.0223 | 0.1378 | 0.0863 | 0.1325 | 0.0567 | 0.0512 | 0.0821 | 0.0785 | 0.0805 |
| 2R | 0.0993 | 0.0767 | 0.1335 | 0.1535 | 0.1334 | 0.0866 | 0.0372 | 0.0530 | 0.0929 | 0.0966 |
| 3L | 0.0611 | 0.0115 | 0.0457 | 0.0329 | 0.1867 | 0.0208 | 0.0248 | 0.0179 | 0.0289 | 0.0502 |
| 3R | 0.0789 | 0.0353 | 0.1108 | 0.0652 | 0.1821 | 0.0727 | 0.0341 | 0.0200 | 0.0689 | 0.0749 |
| genome-wide | 0.0820 | 0.0419 | 0.1119 | 0.0914 | 0.1564 | 0.0651 | 0.0370 | 0.0429 | 0.0736 | 0.0786 |
| | partial soft (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.0816 | 0.0274 | 0.0533 | 0.1026 | 0.0468 | 0.0385 | 0.1127 | 0.0987 | 0.0674 | 0.0702 |
| 2R | 0.0643 | 0.0388 | 0.0673 | 0.0530 | 0.0455 | 0.0280 | 0.0987 | 0.1114 | 0.0587 | 0.0634 |
| 3L | 0.0576 | 0.0257 | 0.0645 | 0.0833 | 0.0484 | 0.0203 | 0.0742 | 0.1004 | 0.0610 | 0.0593 |
| 3R | 0.0682 | 0.0285 | 0.0632 | 0.1540 | 0.0492 | 0.0251 | 0.0983 | 0.1182 | 0.0657 | 0.0756 |
| genome-wide | 0.0678 | 0.0312 | 0.0628 | 0.0979 | 0.0473 | 0.0279 | 0.0971 | 0.1088 | 0.0653 | 0.0676 |
| | partial soft – linked (proportion) corrected for false discovery | | | | | | | | | |
| 2L | 0.1723 | 0.1157 | 0.2884 | 0.4666 | 0.1327 | 0.1322 | 0.3085 | 0.2866 | 0.2294 | 0.2379 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **2R** | 0.1501 | 0.2584 | 0.2687 | 0.4003 | 0.1806 | 0.1097 | 0.2546 | 0.3147 | 0.2565 | 0.2421 |
| **3L** | 0.1534 | 0.1259 | 0.2874 | 0.4603 | 0.1588 | 0.0874 | 0.1885 | 0.2433 | 0.1737 | 0.2132 |
| **3R** | 0.1571 | 0.1435 | 0.2951 | 0.3931 | 0.1887 | 0.1225 | 0.2225 | 0.2550 | 0.2056 | 0.2222 |
| **genome-wide** | 0.1572 | 0.1723 | 0.2836 | 0.4230 | 0.1696 | 0.1141 | 0.2446 | 0.2787 | 0.2085 | 0.2304 |
| ***neutral*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 1,224.2 | 2,022.7 | 940.1 | 120.6 | 941.3 | 936.4 | 137.4 | 676.2 | 938.3 | 874.9 |
| **2R** | 1,919.5 | 1,866.2 | 1,508.9 | 53.4 | 1,115.0 | 1,828.0 | 187.0 | 1,231.0 | 1,369.9 | 1,213.6 |
| **3L** | 1,233.9 | 1,827.4 | 1,157.4 | 46.4 | 679.6 | 1,505.3 | 1,003.8 | 1,140.5 | 1,149.0 | 1,074.3 |
| **3R** | 2,021.8 | 2,633.2 | 1,401.3 | 71.9 | 1,146.7 | 1,848.1 | 1,189.6 | 1,609.5 | 1,505.4 | 1,490.3 |
| **genome-wide** | 6,399.3 | 8,349.5 | 5,007.8 | 292.3 | 3,882.6 | 6,117.8 | 2,517.8 | 4,657.1 | 4,832.5 | 4,653.0 |
| ***completed hard*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 0.0 | 0.0 | 0.0 | 1.9 | 1.0 | 0.0 | 0.0 | 1.0 | 0.0 | 0.5 |
| **2R** | 4.0 | 2.0 | 1.0 | -0.1 | 1.0 | 1.0 | 4.0 | 1.0 | 1.0 | 1.7 |
| **3L** | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.0 | 0.0 | 0.0 | 0.4 |
| **3R** | 0.0 | 3.0 | 2.0 | -0.1 | 2.0 | 1.0 | 1.0 | 3.0 | 1.5 | 1.5 |
| **genome-wide** | 4.0 | 6.0 | 3.0 | 1.7 | 4.0 | 2.0 | 7.0 | 5.0 | 4.0 | 4.1 |
| ***completed hard – linked*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 1.0 | -3.0 | 5.0 | 11.0 | 0.0 | 5.0 | 0.0 | 2.0 | 1.5 | 2.6 |
| **2R** | 19.0 | 4.3 | 6.0 | 17.0 | 7.0 | 4.0 | 8.0 | 11.0 | 7.5 | 9.5 |
| **3L** | 2.0 | 1.3 | 1.0 | 8.0 | 1.0 | 3.0 | 1.0 | 2.0 | 1.7 | 2.4 |
| **3R** | 10.0 | 4.7 | 8.0 | 3.0 | 1.0 | 0.0 | 0.0 | 5.0 | 3.9 | 4.0 |
| **genome-wide** | 32.0 | 7.3 | 20.0 | 39.0 | 9.0 | 12.0 | 9.0 | 20.0 | 16.0 | 18.5 |
| ***completed soft*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 124.0 | 72.8 | 51.2 | 83.2 | 87.8 | 132.8 | 178.3 | 138.4 | 105.9 | 108.6 |
| **2R** | 284.4 | 125.9 | 114.5 | 128.2 | 268.5 | 207.0 | 353.0 | 271.7 | 237.7 | 219.1 |
| **3L** | 93.8 | 48.2 | 57.5 | 120.3 | 62.2 | 74.3 | 133.9 | 116.8 | 84.1 | 88.4 |
| **3R** | 123.6 | 82.6 | 63.8 | 146.9 | 96.1 | 144.4 | 242.9 | 175.0 | 134.0 | 134.4 |
| **genome-wide** | 625.8 | 329.6 | 287.0 | 478.6 | 514.5 | 558.6 | 908.0 | 701.9 | 536.6 | 550.5 |
| ***completed soft – linked*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 251.7 | 231.8 | 377.5 | 753.3 | 372.2 | 912.2 | 1,019.5 | 580.9 | 479.2 | 562.4 |
| **2R** | 493.5 | 726.9 | 601.4 | 1,341.8 | 952.7 | 1,273.8 | 1,998.8 | 764.6 | 858.7 | 1,019.2 |
| **3L** | 150.6 | 211.2 | 316.6 | 1,064.0 | 207.4 | 410.8 | 526.9 | 380.2 | 348.4 | 408.4 |
| **3R** | 256.6 | 343.6 | 517.4 | 1,441.4 | 263.1 | 853.2 | 971.7 | 629.3 | 573.4 | 659.5 |
| **genome-wide** | 1,152.4 | 1,513.6 | 1,812.9 | 4,600.6 | 1,795.3 | 3,450.0 | 4,516.9 | 2,355.1 | 2,084.0 | 2,649.6 |
| ***partial hard*** *(count)* corrected for false discovery | | | | | | | | | | |
| **2L** | 68.8 | 29.0 | 133.1 | 102.8 | 348.2 | 89.0 | 108.0 | 121.3 | 105.4 | 125.0 |
| **2R** | 150.1 | 109.0 | 258.5 | 415.9 | 387.7 | 161.0 | 121.0 | 134.8 | 155.5 | 217.2 |
| **3L** | 33.8 | 18.0 | 34.8 | 33.9 | 345.0 | 17.0 | 28.0 | 29.9 | 31.8 | 67.5 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **3R** | 83.0 | 53.0 | 155.6 | 78.9 | 608.6 | 120.0 | 74.0 | 44.4 | 80.9 | 152.2 |
| **genome-wide** | 335.6 | 209.0 | 582.0 | 631.4 | 1,689.4 | 387.0 | 331.0 | 330.3 | 361.3 | 562.0 |
| | ***partial hard – linked*** *(count)* <br> *corrected for false discovery* | | | | | | | | | |
| **2L** | 186.1 | 63.0 | 399.1 | 268.9 | 337.0 | 152.3 | 140.0 | 234.3 | 210.2 | 222.6 |
| **2R** | 415.3 | 347.0 | 626.5 | 763.9 | 569.0 | 387.7 | 163.0 | 245.8 | 401.5 | 439.8 |
| **3L** | 127.1 | 29.0 | 118.8 | 99.0 | 399.0 | 48.0 | 59.0 | 46.9 | 79.0 | 115.8 |
| **3R** | 282.9 | 139.0 | 448.6 | 292.9 | 665.0 | 276.6 | 131.0 | 81.4 | 279.8 | 289.7 |
| **genome-wide** | 1,011.4 | 578.0 | 1,593.0 | 1,424.7 | 1,970.0 | 864.5 | 493.0 | 608.3 | 938.0 | 1,067.9 |
| | ***partial soft*** *(count)* <br> *corrected for false discovery* | | | | | | | | | |
| **2L** | 202.9 | 77.4 | 154.2 | 319.4 | 119.0 | 103.3 | 308.2 | 281.7 | 178.5 | 195.8 |
| **2R** | 269.1 | 175.7 | 315.8 | 264.0 | 194.0 | 125.2 | 432.9 | 516.5 | 266.5 | 286.7 |
| **3L** | 119.7 | 64.8 | 167.9 | 250.2 | 103.4 | 46.8 | 176.7 | 262.6 | 143.8 | 149.0 |
| **3R** | 244.7 | 112.3 | 256.0 | 692.3 | 179.5 | 95.5 | 377.7 | 480.2 | 250.3 | 304.8 |
| **genome-wide** | 836.4 | 430.2 | 893.8 | 1,525.9 | 596.0 | 370.8 | 1,295.5 | 1,541.0 | 865.1 | 936.2 |
| | ***partial soft – linked*** *(count)* <br> *corrected for false discovery* | | | | | | | | | |
| **2L** | 428.4 | 326.3 | 834.8 | 1,452.9 | 337.6 | 355.1 | 843.7 | 818.1 | 623.2 | 674.6 |
| **2R** | 628.0 | 1,169.9 | 1,261.4 | 1,991.9 | 770.1 | 491.3 | 1,116.3 | 1,458.7 | 1,143.1 | 1,110.9 |
| **3L** | 319.2 | 317.0 | 747.9 | 1,383.3 | 339.4 | 201.7 | 448.7 | 636.3 | 394.1 | 549.2 |
| **3R** | 563.5 | 564.6 | 1,194.3 | 1,766.8 | 689.1 | 466.3 | 855.1 | 1,036.2 | 772.1 | 892.0 |
| **genome-wide** | 1,939.0 | 2,377.9 | 4,038.5 | 6,594.8 | 2,136.2 | 1,514.3 | 3,263.8 | 3,949.3 | 2,820.8 | 3,226.7 |

**Table S4.** Enrichments of selective sweeps within DNA regions for each empirical mosquito population dataset.

| | | AOM | BFM | BFS | CMS | GAS | GNS | GWA | UGS |
|---|---|---|---|---|---|---|---|---|---|
| | | *all four sweep states* | | | | | | | |
| **gene** | count | 1177 | 820 | 1173 | 1530 | 1636 | 1028 | 1698 | 1839 |
| | enrichment | 1.11 | 1.24 | 1.19 | 1.13 | 1.08 | 1.14 | 1.15 | 1.18 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **mRNA** | count | 1176 | 819 | 1171 | 1529 | 1634 | 1028 | 1697 | 1836 |
| | enrichment | 1.11 | 1.24 | 1.19 | 1.13 | 1.08 | 1.14 | 1.15 | 1.18 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **exon** | count | 919 | 700 | 951 | 1230 | 1280 | 824 | 1365 | 1506 |
| | enrichment | 1.18 | 1.44 | 1.31 | 1.23 | 1.14 | 1.24 | 1.25 | 1.31 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **CDS** | count | 887 | 685 | 930 | 1198 | 1231 | 798 | 1325 | 1468 |
| | enrichment | 1.19 | 1.48 | 1.36 | 1.26 | 1.16 | 1.26 | 1.28 | 1.35 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **5' UTR** | count | 338 | 265 | 358 | 445 | 446 | 302 | 507 | 537 |
| | enrichment | 1.24 | 1.56 | 1.41 | 1.28 | 1.16 | 1.30 | 1.34 | 1.34 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| **3' UTR** | count | 312 | 247 | 343 | 414 | 416 | 278 | 440 | 502 |
| | enrichment | 1.34 | 1.70 | 1.59 | 1.38 | 1.26 | 1.40 | 1.37 | 1.47 |
| | *p*-value | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| | | *completed hard* | | | | | | | |
| **gene** | count | 1 | 5 | 2 | 2 | 2 | 1 | 4 | 4 |
| | enrichment | 0.45 | 1.68 | 1.30 | 1.71 | 0.93 | 0.95 | 1.15 | 1.51 |
| | *p*-value | 0.9278 | 0.1034 | 0.5170 | 0.5043 | 0.7459 | 0.7780 | 0.5054 | 0.2250 |
| **mRNA** | count | 1 | 5 | 2 | 2 | 2 | 1 | 4 | 4 |
| | enrichment | 0.45 | 1.69 | 1.30 | 1.71 | 0.93 | 0.95 | 1.15 | 1.52 |
| | *p*-value | 0.9276 | 0.1020 | 0.5143 | 0.5043 | 0.7436 | 0.7770 | 0.5038 | 0.2237 |
| **exon** | count | 1 | 3 | 2 | 2 | 2 | 1 | 4 | 4 |
| | enrichment | 0.59 | 1.35 | 1.78 | 2.45 | 1.28 | 1.28 | 1.50 | 2.09 |
| | *p*-value | 0.8484 | 0.3910 | 0.3126 | 0.2786 | 0.5070 | 0.6298 | 0.2734 | 0.0762 |
| **CDS** | count | 1 | 3 | 2 | 2 | 2 | 1 | 4 | 4 |
| | enrichment | 0.62 | 1.42 | 1.87 | 2.61 | 1.35 | 1.34 | 1.58 | 2.21 |
| | *p*-value | 0.8288 | 0.3574 | 0.2881 | 0.2549 | 0.4743 | 0.6087 | 0.2387 | 0.0647 |
| **5' UTR** | count | 0 | 2 | 1 | 0 | 1 | 0 | 3 | 1 |
| | enrichment | 0.00 | 2.56 | 2.55 | 0.00 | 1.80 | 0.00 | 3.17 | 1.48 |
| | *p*-value | 1.0000 | 0.1804 | 0.3424 | 1.0000 | 0.4523 | 1.0000 | 0.0652 | 0.5172 |
| **3' UTR** | count | 0 | 2 | 1 | 0 | 1 | 1 | 0 | 2 |
| | enrichment | 0.00 | 2.94 | 2.92 | 0.00 | 2.13 | 4.15 | 0.00 | 3.50 |
| | *p*-value | 1.0000 | 0.1430 | 0.3015 | 1.0000 | 0.3906 | 0.2259 | 1.0000 | 0.1017 |
| | | *completed soft* | | | | | | | |
| **gene** | count | 485 | 345 | 283 | 376 | 425 | 521 | 715 | 617 |
| | enrichment | 1.25 | 1.70 | 1.83 | 1.57 | 1.41 | 1.36 | 1.41 | 1.47 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| **mRNA** | count | 485 | 345 | 283 | 376 | 425 | 521 | 715 | 617 |
| | enrichment | 1.25 | 1.70 | 1.83 | 1.58 | 1.41 | 1.36 | 1.41 | 1.48 |
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| **exon** | count | 424 | 335 | 276 | 356 | 394 | 459 | 665 | 582 |
| | enrichment | 1.47 | 2.24 | 2.39 | 1.99 | 1.76 | 1.62 | 1.77 | 1.88 |
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| **CDS** | count | 416 | 334 | 274 | 351 | 389 | 453 | 653 | 575 |
| | enrichment | 1.52 | 2.35 | 2.51 | 2.08 | 1.83 | 1.68 | 1.83 | 1.96 |
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| **5' UTR** | count | 157 | 126 | 96 | 124 | 141 | 172 | 239 | 213 |
| | enrichment | 1.55 | 2.40 | 2.37 | 2.01 | 1.78 | 1.74 | 1.83 | 1.96 |
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| **3' UTR** | count | 153 | 131 | 98 | 131 | 137 | 163 | 245 | 208 |
| | enrichment | 1.77 | 2.93 | 2.86 | 2.46 | 2.03 | 1.93 | 2.20 | 2.26 |
| | *p*-value | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 | ≤0.0001 |
| | | | | | *partial hard* | | | | |
| **gene** | count | 180 | 99 | 358 | 375 | 845 | 210 | 189 | 206 |
| | enrichment | 0.99 | 0.89 | 1.13 | 1.09 | 0.98 | 1.01 | 1.05 | 1.12 |
| | *p*-value | 0.5989 | 0.9251 | 0.0018 | 0.0364 | 0.7931 | 0.4632 | 0.2261 | 0.0305 |
| **mRNA** | count | 180 | 99 | 357 | 374 | 844 | 210 | 189 | 206 |
| | enrichment | 0.99 | 0.89 | 1.13 | 1.08 | 0.98 | 1.01 | 1.05 | 1.12 |
| | *p*-value | 0.5896 | 0.9219 | 0.0020 | 0.0392 | 0.7849 | 0.4540 | 0.2215 | 0.0294 |
| **exon** | count | 116 | 74 | 250 | 290 | 612 | 141 | 127 | 153 |
| | enrichment | 0.86 | 0.90 | 1.08 | 1.13 | 0.96 | 0.92 | 0.96 | 1.13 |
| | *p*-value | 0.9707 | 0.8584 | 0.1037 | 0.0141 | 0.8605 | 0.8407 | 0.6916 | 0.0487 |
| **CDS** | count | 110 | 69 | 244 | 282 | 584 | 130 | 122 | 150 |
| | enrichment | 0.86 | 0.88 | 1.11 | 1.16 | 0.97 | 0.90 | 0.98 | 1.18 |
| | *p*-value | 0.9685 | 0.8856 | 0.0415 | 0.0060 | 0.8130 | 0.9043 | 0.6225 | 0.0169 |
| **5' UTR** | count | 39 | 30 | 108 | 103 | 210 | 50 | 48 | 53 |
| | enrichment | 0.82 | 1.01 | 1.30 | 1.09 | 0.97 | 0.92 | 1.02 | 1.10 |
| | *p*-value | 0.9118 | 0.4890 | 0.0046 | 0.2032 | 0.6747 | 0.7255 | 0.4641 | 0.2741 |
| **3' UTR** | count | 42 | 26 | 101 | 105 | 189 | 42 | 34 | 50 |
| | enrichment | 1.04 | 1.03 | 1.44 | 1.33 | 1.01 | 0.91 | 0.86 | 1.25 |
| | *p*-value | 0.4317 | 0.4620 | 0.0003 | 0.0053 | 0.4343 | 0.7325 | 0.8156 | 0.0725 |
| | | | | | *partial soft* | | | | |
| **gene** | count | 511 | 371 | 530 | 777 | 364 | 296 | 790 | 1012 |
| | enrichment | 1.05 | 1.08 | 1.04 | 1.01 | 1.06 | 0.96 | 1.01 | 1.07 |
| | *p*-value | 0.0684 | 0.0298 | 0.1025 | 0.3927 | 0.0761 | 0.8089 | 0.3293 | 0.0019 |
| **mRNA** | count | 510 | 370 | 529 | 777 | 363 | 296 | 789 | 1009 |
| | enrichment | 1.05 | 1.08 | 1.04 | 1.01 | 1.06 | 0.97 | 1.01 | 1.07 |
| | *p*-value | 0.0692 | 0.0323 | 0.1045 | 0.3704 | 0.0809 | 0.7996 | 0.3228 | 0.0023 |
| **exon** | count | 378 | 288 | 423 | 582 | 272 | 223 | 569 | 767 |
| | enrichment | 1.06 | 1.13 | 1.12 | 1.02 | 1.07 | 0.98 | 0.99 | 1.10 |
| | *p*-value | 0.0903 | 0.0066 | 0.0021 | 0.2958 | 0.0884 | 0.6337 | 0.6480 | 0.0014 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| **CDS** | **count** | 360 | <u>279</u> | <u>410</u> | 563 | 256 | 214 | 546 | <u>739</u> |
| | enrichment | 1.06 | <u>1.16</u> | <u>1.15</u> | 1.05 | 1.06 | 0.99 | 1.00 | <u>1.12</u> |
| | *p*-value | 0.0885 | <u>0.0023</u> | <u>0.0008</u> | 0.1591 | 0.1288 | 0.5577 | 0.5153 | <u>0.0004</u> |
| **5' UTR** | **count** | 142 | <u>107</u> | <u>153</u> | 218 | 94 | 80 | 217 | <u>270</u> |
| | enrichment | 1.14 | <u>1.21</u> | <u>1.17</u> | 1.11 | 1.07 | 1.02 | 1.09 | <u>1.11</u> |
| | *p*-value | 0.0535 | <u>0.0244</u> | <u>0.0253</u> | 0.0802 | 0.2633 | 0.4512 | 0.0966 | <u>0.0348</u> |
| **3' UTR** | **count** | 117 | 88 | <u>143</u> | 178 | 89 | 72 | 161 | <u>242</u> |
| | enrichment | 1.10 | 1.17 | <u>1.28</u> | 1.05 | 1.18 | 1.07 | 0.94 | <u>1.17</u> |
| | *p*-value | 0.1448 | 0.0834 | <u>0.0015</u> | 0.2652 | 0.0557 | 0.2863 | 0.7917 | <u>0.0051</u> |

Significant values (*i.e. p* < 0.05) underlined.

**Table S5.** Enrichments of selective sweeps within groupings of insecticide resistance genes for each empirical mosquito population dataset.

| | | AOM | BFM | BFS | CMS | GAS | GNS | GWA | UGS |
|---|---|---|---|---|---|---|---|---|---|
| | | *all four sweep states* | | | | | | | |
| metabolism | count | 67 | 58 | 60 | 88 | 69 | 57 | 75 | 95 |
| | enrichment | 1.57 | 2.16 | 1.50 | 1.65 | 1.25 | 1.61 | 1.35 | 1.57 |
| | *p*-value | 0.0011 | <0.0001 | 0.0048 | <0.0001 | 0.0464 | 0.0018 | 0.0076 | 0.0001 |
| target site | count | 9 | 9 | 5 | 7 | 7 | 7 | 8 | 9 |
| | enrichment | 1.95 | 2.90 | 1.16 | 1.38 | 1.12 | 1.69 | 1.28 | 1.44 |
| | *p*-value | 0.0132 | 0.0007 | 0.4434 | 0.2087 | 0.4439 | 0.0823 | 0.2509 | 0.1096 |
| behavior | count | 18 | 19 | 15 | 20 | 20 | 18 | 18 | 20 |
| | enrichment | 1.73 | 2.63 | 1.42 | 1.51 | 1.37 | 2.04 | 1.24 | 1.26 |
| | *p*-value | 0.0507 | 0.0039 | 0.1619 | 0.1041 | 0.1518 | 0.0187 | 0.2480 | 0.2231 |
| cuticular | count | 2 | 1 | 2 | 6 | 5 | 2 | 5 | 7 |
| | enrichment | 0.82 | 0.60 | 0.87 | 1.77 | 1.49 | 1.02 | 1.62 | 1.94 |
| | *p*-value | 0.7046 | 0.8049 | 0.6813 | 0.1215 | 0.2408 | 0.5782 | 0.1921 | 0.0603 |
| | | *completed hard* | | | | | | | |
| metabolism | count | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 |
| | enrichment | 0.00 | 0.00 | 26.63 | 0.00 | 0.00 | 0.00 | 0.00 | 8.64 |
| | *p*-value | 1.0000 | 1.0000 | 0.0121 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 0.0932 |
| target site | count | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | enrichment | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | *p*-value | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 |
| behavior | count | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 3 |
| | enrichment | 0.00 | 0.00 | 80.00 | 0.00 | 0.00 | 68.97 | 45.56 | 94.64 |
| | *p*-value | 1.0000 | 1.0000 | 0.0047 | 1.0000 | 1.0000 | 0.0109 | 0.0076 | 0.0020 |
| cuticular | count | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | enrichment | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | *p*-value | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 | 1.0000 |
| | | *completed soft* | | | | | | | |
| metabolism | count | 32 | 23 | 18 | 23 | 23 | 32 | 45 | 33 |
| | enrichment | 1.93 | 2.68 | 2.62 | 2.12 | 1.78 | 1.97 | 2.13 | 1.87 |
| | *p*-value | 0.0046 | 0.0008 | 0.0038 | 0.0036 | 0.0179 | 0.0021 | <0.0001 | 0.0053 |
| target site | count | 5 | 5 | 0 | 3 | 4 | 5 | 5 | 3 |
| | enrichment | 2.59 | 4.51 | 0.00 | 2.26 | 2.41 | 2.45 | 1.85 | 1.42 |
| | *p*-value | 0.0298 | 0.0025 | 1.0000 | 0.1322 | 0.0701 | 0.0390 | 0.1085 | 0.3543 |
| behavior | count | 11 | 4 | 2 | 10 | 12 | 9 | 7 | 9 |
| | enrichment | 2.79 | 1.79 | 1.13 | 3.91 | 3.89 | 2.29 | 1.29 | 1.98 |
| | *p*-value | 0.0180 | 0.2175 | 0.4666 | 0.0040 | 0.0025 | 0.0512 | 0.3263 | 0.0908 |
| cuticular | count | 1 | 0 | 0 | 0 | 1 | 2 | 5 | 4 |
| | enrichment | 1.06 | 0.00 | 0.00 | 0.00 | 1.54 | 2.24 | 4.42 | 3.84 |
| | *p*-value | 0.5901 | 1.0000 | 1.0000 | 1.0000 | 0.4597 | 0.2233 | 0.0075 | 0.0307 |
| | | *partial hard* | | | | | | | |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| metabolism | count | 11 | 8 | 18 | <u>36</u> | 32 | 10 | 8 | <u>24</u> |
| | enrichment | 1.40 | 1.77 | 1.39 | <u>2.58</u> | 1.02 | 1.27 | 1.16 | <u>3.27</u> |
| | *p*-value | 0.1944 | 0.1293 | 0.1453 | <u>0.0002</u> | 0.4736 | 0.2850 | 0.3799 | <u>0.0001</u> |
| target site | count | 0 | 0 | 1 | <u>4</u> | 3 | 1 | 0 | 1 |
| | enrichment | 0.00 | 0.00 | 0.66 | <u>2.70</u> | 0.80 | 1.11 | 0.00 | 1.07 |
| | *p*-value | 1.0000 | 1.0000 | 0.8033 | <u>0.0479</u> | 0.7734 | 0.6117 | 1.0000 | 0.6268 |
| behavior | count | 1 | 2 | 2 | 1 | 8 | 1 | 1 | 0 |
| | enrichment | 0.52 | 1.50 | 0.59 | 0.27 | 0.93 | 0.50 | 0.62 | 0.00 |
| | *p*-value | 0.7638 | 0.3395 | 0.7553 | 0.9470 | 0.5637 | 0.7603 | 0.6956 | 1.0000 |
| cuticular | count | 0 | 1 | 0 | 1 | 5 | 0 | 0 | 1 |
| | enrichment | 0.00 | 4.10 | 0.00 | 1.43 | 2.37 | 0.00 | 0.00 | 1.95 |
| | *p*-value | 1.0000 | 0.2027 | 1.0000 | 0.4852 | 0.0684 | 1.0000 | 1.0000 | 0.3747 |
| | | *partial soft* | | | | | | | |
| metabolism | count | 25 | <u>27</u> | 25 | 31 | 19 | 16 | 27 | 45 |
| | enrichment | 1.22 | <u>1.86</u> | 1.14 | 1.04 | 1.30 | 1.22 | 0.86 | 1.15 |
| | *p*-value | 0.2060 | <u>0.0095</u> | 0.2976 | 0.4337 | 0.1829 | 0.2658 | 0.7766 | 0.2125 |
| target site | count | 4 | 4 | 4 | 2 | 0 | 2 | 3 | 5 |
| | enrichment | 1.59 | 2.18 | 1.55 | 0.68 | 0.00 | 1.15 | 0.79 | 1.15 |
| | *p*-value | 0.2227 | 0.0966 | 0.2479 | 0.8377 | 1.0000 | 0.5334 | 0.7865 | 0.4586 |
| behavior | count | 6 | <u>13</u> | 9 | 9 | 2 | 7 | 9 | 10 |
| | enrichment | 1.19 | <u>3.36</u> | 1.56 | 1.27 | 0.55 | 2.23 | 1.11 | 0.95 |
| | *p*-value | 0.3837 | <u>0.0043</u> | 0.1779 | 0.3076 | 0.7908 | 0.0840 | 0.4277 | 0.5751 |
| cuticular | count | 1 | 0 | 2 | 5 | 0 | 0 | 0 | 3 |
| | enrichment | 0.82 | 0.00 | 1.58 | 2.36 | 0.00 | 0.00 | 0.00 | 1.32 |
| | *p*-value | 0.6906 | 1.0000 | 0.3598 | 0.0728 | 1.0000 | 1.0000 | 1.0000 | 0.3991 |

Significant values (*i.e. p* < 0.05) underlined.

**Table S6.** Statistically significant enrichments of selective sweeps within GO term annotations for each empirical mosquito population

|  |  | A O M |  |  |
|---|---|---|---|---|
| GO term | function | count | enrichment | *q* -value |

*all four sweep states*
*:molecular function*

| GO term | function | count | enrichment | q-value |
|---|---|---|---|---|
| GO:0005524 | ATP binding | 78 | 1.46 | 0.03875 |
| GO:0003676 | nucleic acid binding | 74 | 1.53 | 0.02583 |
| GO:0005488 | binding | 31 | 1.78 | 0.02583 |
| GO:0003723 | RNA binding | 29 | 1.80 | 0.02583 |

*all four sweep states*
*:cellular components*

*completed soft*
*:cellular components*

| GO:0005886 | plasma membrane | 27 | 2.15 | 0.03780 |
|---|---|---|---|---|
| GO:0030286 | dynein complex | 6 | 4.21 | 0.03780 |
| GO:0005847 | mRNA cleavage and p | 4 | 8.14 | 0.03780 |
| GO:0005737 | cytoplasm | 39 | 1.90 | 0.03780 |
| GO:0005694 | chromosome | 6 | 5.54 | 0.02835 |
| GO:0016021 | integral component of | 121 | 1.56 | <0.01260 |
| GO:0005634 | nucleus | 60 | 1.80 | <0.01260 |
| GO:0016020 | membrane | 42 | 1.91 | <0.01260 |

*:molecular function*

*:molecular function*

| GO:0005524 | ATP binding | 40 | 1.90 | 0.01598 |
|---|---|---|---|---|
| GO:0005488 | binding | 18 | 2.50 | 0.01598 |
| GO:0005515 | protein binding | 99 | 1.68 | <0.01598 |
| GO:0003676 | nucleic acid binding | 50 | 2.60 | <0.01598 |
| GO:0003723 | RNA binding | 19 | 3.04 | <0.01598 |

*completed soft*
*:biological processes*

*:cellular components*

*:molecular function*

dataset.

| GO term | function | B F M count | enrichment | $q$-value | | GO term |
|---------|----------|-------------|------------|-----------|---|---------|
| | | | | | *all four sweep states* | |
| | | | | | *:biological processes* | |
| GO:0030286 | dynein complex | 7 | 3.60 | 0.03720 | | GO:0006508 |
| GO:0005737 | cytoplasm | 57 | 1.75 | 0.00744 | | GO:0000398 |
| GO:0016020 | membrane | 63 | 1.77 | 0.00744 | *:cellular components* | |
| GO:0005634 | nucleus | 83 | 1.54 | <0.00744 | | GO:0005840 |
| GO:0016021 | integral component of | 199 | 1.57 | <0.00744 | | GO:0005737 |
| GO:0005887 | integral component of | 25 | 2.37 | <0.00744 | | GO:0005622 |
| | | | | | | GO:0016021 |
| GO:0003723 | RNA binding | 22 | 2.08 | 0.03875 | | GO:0016020 |
| GO:0005524 | ATP binding | 55 | 1.67 | 0.02214 | | GO:0005634 |
| GO:0005506 | iron ion binding | 18 | 3.24 | 0.02214 | | GO:0005654 |
| GO:0005515 | protein binding | 181 | 1.86 | <0.01550 | *:molecular function* | |
| GO:0008270 | zinc ion binding | 57 | 1.88 | <0.01550 | | GO:0005524 |
| GO:0003676 | nucleic acid binding | 78 | 2.43 | <0.01550 | | GO:0005509 |
| GO:0005488 | binding | 29 | 2.49 | <0.01550 | | GO:0005515 |
| GO:0016787 | hydrolase activity | 15 | 3.14 | <0.01550 | | GO:0003676 |
| | | | | | | GO:0005488 |
| | | | | | | GO:0003723 |
| GO:0007165 | signal transduction | 20 | 4.39 | <0.03513 | | GO:0004252 |
| GO:0006508 | proteolysis | 29 | 4.84 | <0.03513 | *completed soft* | |
| GO:0000398 | mRNA splicing, via spl | 8 | 7.27 | <0.03513 | *:biological processes* | |
| | | | | | | GO:0045944 |
| GO:0005852 | eukaryotic translation | 3 | 11.92 | 0.03860 | | GO:0006508 |
| GO:0005847 | mRNA cleavage and p | 3 | 13.63 | 0.02573 | | GO:0007165 |
| GO:0005763 | mitochondrial small r | 3 | 13.57 | 0.02413 | | GO:0007018 |
| GO:0005840 | ribosome | 7 | 4.66 | 0.01654 | | GO:0000398 |
| GO:0005654 | nucleoplasm | 5 | 11.08 | 0.01654 | *:cellular components* | |

| GO:0005622 | intracellular | 20 | 2.96 | 0.00772 | | GO:0005840 |
|---|---|---|---|---|---|---|
| GO:0016021 | integral component of | 88 | 2.10 | <0.00772 | | GO:0030286 |
| GO:0016020 | membrane | 30 | 2.52 | <0.00772 | | GO:0016020 |
| GO:0005634 | nucleus | 49 | 2.74 | <0.00772 | | GO:0016021 |
| GO:0005737 | cytoplasm | 29 | 2.75 | <0.00772 | | GO:0005634 |
| | | | | | | GO:0005737 |
| GO:0016491 | oxidoreductase activit | 12 | 3.70 | 0.04368 | | GO:0005622 |
| GO:0004812 | aminoacyl-tRNA ligase | 4 | 8.16 | 0.03609 | | GO:0005654 |
| GO:0003735 | structural constituent | 8 | 4.60 | 0.02750 | *:molecular function* | |
| GO:0004177 | aminopeptidase activi | 3 | 16.04 | 0.02357 | | |
| GO:0003682 | chromatin binding | 6 | 5.64 | 0.01904 | | GO:0008234 |
| GO:0000166 | nucleotide binding | 8 | 5.66 | 0.01904 | | GO:0030170 |
| GO:0004252 | serine-type endopepti | 17 | 4.73 | 0.00750 | | GO:0008270 |
| GO:0005506 | iron ion binding | 11 | 6.25 | 0.00750 | | GO:0005515 |
| GO:0005085 | guanyl-nucleotide exc | 4 | 7.35 | 0.00750 | | GO:0005524 |
| GO:0046872 | metal ion binding | 19 | 2.93 | <0.00750 | | GO:0003676 |
| GO:0005515 | protein binding | 108 | 3.28 | <0.00750 | | GO:0003723 |
| GO:0008270 | zinc ion binding | 33 | 3.30 | <0.00750 | | GO:0005488 |
| GO:0005524 | ATP binding | 38 | 3.46 | <0.00750 | | GO:0016887 |
| GO:0003723 | RNA binding | 15 | 4.26 | <0.00750 | | GO:0003777 |
| GO:0016887 | ATPase activity | 10 | 4.37 | <0.00750 | | GO:0035091 |
| GO:0005488 | binding | 18 | 4.53 | <0.00750 | | |
| GO:0003676 | nucleic acid binding | 51 | 4.79 | <0.00750 | | |

| | B | F | S | | | | C | M |
|---|---|---|---|---|---|---|---|---|
| function | | count | enrichment | *q* -value | | GO term | function | count |
| | | | | | *all four sweep states* | | | |
| | | | | | *:biological processes* | | | |
| proteolysis | | 57 | 2.15 | <0.04905 | | GO:0006508 | proteolysis | 70 |
| mRNA splicing, via spl | | 15 | 2.97 | <0.04905 | | GO:0000398 | mRNA splicing, via spl | 16 |
| | | | | | *:cellular components* | | | |
| ribosome | | 17 | 2.41 | 0.02126 | | GO:0005634 | nucleus | 128 |
| cytoplasm | | 73 | 1.54 | 0.01240 | | GO:0016020 | membrane | 91 |
| intracellular | | 51 | 1.71 | 0.01240 | | GO:0016021 | integral component of | 307 |
| integral component of | | 263 | 1.44 | <0.00930 | | GO:0005681 | spliceosomal complex | 9 |
| membrane | | 77 | 1.49 | <0.00930 | | *:molecular function* | | |
| nucleus | | 119 | 1.53 | <0.00930 | | | | |
| nucleoplasm | | 9 | 4.93 | <0.00930 | | GO:0005524 | ATP binding | 86 |
| | | | | | | GO:0016887 | ATPase activity | 22 |
| | | | | | | GO:0005515 | protein binding | 250 |
| ATP binding | | 70 | 1.44 | 0.04429 | | GO:0008270 | zinc ion binding | 91 |
| calcium ion binding | | 39 | 1.64 | 0.02583 | | GO:0003676 | nucleic acid binding | 105 |
| protein binding | | 207 | 1.47 | <0.01550 | | GO:0004252 | serine-type endopept | 49 |
| nucleic acid binding | | 87 | 1.85 | <0.01550 | | *completed soft* | | |
| binding | | 32 | 1.93 | <0.01550 | | *:biological processes* | | |
| RNA binding | | 31 | 1.99 | <0.01550 | | GO:0006511 | ubiquitin-dependent | 7 |
| serine-type endopept | | 39 | 2.49 | <0.01550 | | GO:0016579 | protein deubiquitinat | 6 |
| | | | | | | GO:0000398 | mRNA splicing, via spl | 10 |
| | | | | | *:cellular components* | | | |
| positive regulation of | | 7 | 7.89 | 0.04288 | | GO:0005634 | nucleus | 38 |
| proteolysis | | 20 | 4.39 | <0.02680 | | GO:0005681 | spliceosomal complex | 5 |
| signal transduction | | 19 | 5.27 | <0.02680 | | GO:0016021 | integral component of | 107 |
| microtubule-based m | | 7 | 8.48 | <0.02680 | | GO:0016020 | membrane | 41 |
| mRNA splicing, via spl | | 9 | 11.10 | <0.02680 | | GO:0005886 | plasma membrane | 25 |
| | | | | | *:molecular function* | | | |

| | | | |
|---|---|---|---|
| ribosome | 7 | 5.72 | 0.01945 |
| dynein complex | 5 | 9.22 | 0.01111 |
| membrane | 23 | 2.54 | 0.00648 |
| integral component of | 77 | 2.37 | <0.00648 |
| nucleus | 42 | 3.03 | <0.00648 |
| cytoplasm | 30 | 3.67 | <0.00648 |
| intracellular | 20 | 3.74 | <0.00648 |
| nucleoplasm | 7 | 20.40 | <0.00648 |
| | | | |
| cysteine-type peptida | 5 | 18.48 | 0.04658 |
| pyridoxal phosphate b | 4 | 11.15 | 0.03416 |
| zinc ion binding | 27 | 3.51 | <0.00949 |
| protein binding | 91 | 3.54 | <0.00949 |
| ATP binding | 31 | 3.59 | <0.00949 |
| nucleic acid binding | 31 | 3.69 | <0.00949 |
| RNA binding | 12 | 4.40 | <0.00949 |
| binding | 15 | 4.93 | <0.00949 |
| ATPase activity | 11 | 5.83 | <0.00949 |
| microtubule motor ac | 7 | 9.20 | <0.00949 |
| phosphatidylinositol b | 4 | 13.99 | <0.00949 |

| | | |
|---|---|---|
| GO:0030620 | U2 snRNA binding | 1 |
| GO:0004843 | ubiquitin-specific prot | 4 |
| GO:0005515 | protein binding | 101 |
| GO:0003676 | nucleic acid binding | 38 |
| GO:0005524 | ATP binding | 39 |
| GO:0008270 | zinc ion binding | 36 |
| GO:0005488 | binding | 15 |
| GO:0003723 | RNA binding | 15 |
| GO:0016887 | ATPase activity | 13 |

| S enrichment | S $q$-value | | GO term | function | G count | A enrichment | S $q$-value |
|---|---|---|---|---|---|---|---|
| | | *all four sweep states* *:cellular components* | | | | | |
| 1.94 | <0.04905 | | GO:0005634 | nucleus | 148 | 1.32 | <0.03720 |
| 2.66 | <0.04905 | *:molecular function* | | | | | |
| | | | GO:0005524 | ATP binding | 96 | 1.36 | 0.03875 |
| 1.31 | 0.03720 | | GO:0005515 | protein binding | 248 | 1.26 | <0.02583 |
| 1.39 | 0.02480 | | GO:0003676 | nucleic acid binding | 94 | 1.46 | <0.02583 |
| 1.31 | <0.0186 | | GO:0008270 | zinc ion binding | 90 | 1.49 | <0.02583 |
| 3.51 | <0.0186 | *completed soft* *:cellular components* | | | | | |
| 1.42 | 0.03875 | | GO:0016021 | integral component of | 96 | 1.54 | 0.01895 |
| 2.06 | 0.01550 | | GO:0016020 | membrane | 35 | 2.00 | 0.01895 |
| 1.40 | <0.0155 | | GO:0030286 | dynein complex | 6 | 4.88 | 0.01895 |
| 1.64 | <0.0155 | | GO:0005737 | cytoplasm | 34 | 2.10 | 0.01895 |
| 1.67 | <0.0155 | | GO:0005829 | cytosol | 12 | 3.58 | 0.01895 |
| 2.30 | <0.0155 | | GO:0005634 | nucleus | 70 | 2.56 | <0.01895 |
| | | *:molecular function* | | | | | |
| | | | GO:0005549 | odorant binding | 14 | 5.02 | 0.04700 |
| 6.04 | <0.03727 | | GO:0017137 | Rab GTPase binding | 4 | 6.22 | 0.04494 |
| 7.20 | <0.03727 | | GO:0003723 | RNA binding | 13 | 2.63 | 0.04261 |
| 8.34 | <0.03727 | | GO:0005509 | calcium ion binding | 19 | 2.16 | 0.03995 |
| | | | GO:0016787 | hydrolase activity | 8 | 4.06 | 0.03688 |
| 1.82 | 0.01640 | | GO:0004525 | ribonuclease III activi | 3 | 11.07 | 0.02663 |
| 10.00 | 0.01025 | | GO:0004197 | cysteine-type endope| | 7 | 12.69 | 0.00726 |
| 2.11 | <0.01025 | | GO:0005515 | protein binding | 101 | 2.12 | <0.00726 |
| 2.88 | <0.01025 | | GO:0005524 | ATP binding | 39 | 2.30 | <0.00726 |
| 3.22 | <0.01025 | | GO:0046872 | metal ion binding | 23 | 2.41 | <0.00726 |
| | | | GO:0003677 | DNA binding | 32 | 2.78 | <0.00726 |

| | | GO ID | Term | Count | Fold | P-value |
|---|---|---|---|---|---|---|
| 3333.33 | 0.02950 | GO:0008270 | zinc ion binding | 42 | 2.81 | <0.00726 |
| 9.50 | 0.02213 | GO:0003700 | sequence-specific DN/ | 19 | 2.82 | <0.00726 |
| 2.49 | <0.01264 | GO:0005488 | binding | 17 | 2.89 | <0.00726 |
| 2.85 | <0.01264 | GO:0003676 | nucleic acid binding | 51 | 3.23 | <0.00726 |
| 2.97 | <0.01264 | GO:0004674 | protein serine/threon | 9 | 3.84 | <0.00726 |
| 3.07 | <0.01264 | GO:0008234 | cysteine-type peptida | 7 | 14.78 | <0.00726 |
| 3.28 | <0.01264 | | | | | |
| 3.41 | <0.01264 | | | | | |
| 4.87 | <0.01264 | | | | | |

|  | GO term | function | G N S count | enrichment | $q$ -value |
|---|---|---|---|---|---|
| **all four sweep states** |  |  |  |  |  |
| **:cellular components** |  |  |  |  |  |
|  | GO:0005634 | nucleus | 101 | 1.40 | 0.03720 |
|  | GO:0016021 | integral component of | 237 | 1.38 | <0.03720 |
| **:molecular function** |  |  |  |  |  |
|  | GO:0003676 | nucleic acid binding | 65 | 1.54 | 0.02583 |
|  | GO:0005515 | protein binding | 182 | 1.40 | <0.02583 |
|  | GO:0005524 | ATP binding | 70 | 1.55 | <0.02583 |
| **completed soft** |  |  |  |  |  |
| **:biological processes** |  |  |  |  |  |
|  | GO:0006886 | intracellular protein t | 11 | 3.34 | 0.04136 |
|  | GO:0000398 | mRNA splicing, via spl | 8 | 4.10 | 0.04136 |
|  | GO:0006379 | mRNA cleavage | 4 | 12.77 | 0.04136 |
|  | GO:0006396 | RNA processing | 9 | 4.98 | 0.04136 |
|  | GO:0045944 | positive regulation of | 11 | 4.92 | <0.04136 |
| **:cellular components** |  |  |  |  |  |
|  | GO:0005739 | mitochondrion | 13 | 2.85 | 0.03820 |
|  | GO:0016020 | membrane | 40 | 1.79 | 0.03820 |
|  | GO:0005737 | cytoplasm | 38 | 1.91 | 0.03820 |
|  | GO:0016021 | integral component of | 131 | 1.66 | <0.01910 |
|  | GO:0005634 | nucleus | 72 | 2.16 | <0.01910 |
| **:molecular function** |  |  |  |  |  |
|  | GO:0005515 | protein binding | 116 | 1.90 | <0.01630 |
|  | GO:0008270 | zinc ion binding | 40 | 2.14 | <0.01630 |
|  | GO:0003676 | nucleic acid binding | 45 | 2.34 | <0.01630 |
|  | GO:0003677 | DNA binding | 36 | 2.54 | <0.01630 |
|  | GO:0005524 | ATP binding | 53 | 2.56 | <0.01630 |

*:molecular function*

| | G | W | A | | | GO term |
|---|---|---|---|---|---|---|
| GO term | function | count | enrichment | *q*-value | | |
| | | | | | *all four sweep states* | |
| | | | | | *:cellular components* | |
| GO:0045202 | synapse | 10 | 2.14 | 0.03720 | | GO:0005737 |
| GO:0005737 | cytoplasm | 96 | 1.38 | 0.03720 | | GO:0016020 |
| GO:0005654 | nucleoplasm | 9 | 3.16 | 0.03720 | | GO:0016021 |
| GO:0005634 | nucleus | 146 | 1.29 | 0.01860 | | GO:0005634 |
| GO:0016021 | integral component of | 327 | 1.21 | <0.01860 | *:molecular function* | |
| | | | | | | GO:0004004 |
| GO:0004497 | monooxygenase activi | 22 | 2.15 | 0.04844 | | GO:0003690 |
| GO:0016887 | ATPase activity | 25 | 1.75 | 0.02214 | | GO:0005549 |
| GO:0004252 | serine-type endopept | 44 | 1.83 | 0.02214 | | GO:0003723 |
| GO:0008270 | zinc ion binding | 92 | 1.47 | 0.01550 | | GO:0005524 |
| GO:0003677 | DNA binding | 68 | 1.44 | <0.01550 | | GO:0046872 |
| GO:0005515 | protein binding | 302 | 1.49 | <0.01550 | | GO:0005515 |
| GO:0005524 | ATP binding | 112 | 1.59 | <0.01550 | | GO:0003676 |
| GO:0003676 | nucleic acid binding | 110 | 1.67 | <0.01550 | | GO:0008270 |
| | | | | | | GO:0005488 |
| | | | | | | GO:0004252 |
| GO:0006357 | regulation of transcrip | 16 | 2.27 | 0.04108 | *completed hard* | |
| GO:0006508 | proteolysis | 36 | 2.37 | 0.04108 | *:cellular components* | |
| GO:0007018 | microtubule-based m | 9 | 3.39 | 0.04108 | | GO:0016020 |
| GO:0016579 | protein deubiquitinat | 7 | 3.83 | 0.04108 | *completed soft* | |
| GO:0000278 | mitotic cell cycle | 5 | 6.54 | 0.04108 | *:biological processes* | |
| | | | | | | GO:0007155 |
| GO:0005886 | plasma membrane | 33 | 1.91 | 0.03192 | | GO:0006396 |
| GO:0005829 | cytosol | 15 | 2.45 | 0.02785 | | GO:0006508 |
| GO:0012505 | endomembrane syste | 5 | 5.10 | 0.02681 | | GO:0007165 |
| GO:0005694 | chromosome | 6 | 4.57 | 0.02553 | | GO:0006355 |

| GO:0005622 | intracellular | 30 | 1.88 | 0.01436 | | GO:0007018 |
|---|---|---|---|---|---|---|
| GO:0005813 | centrosome | 6 | 4.65 | 0.01436 | | GO:0000398 |
| GO:0016021 | integral component of | 169 | 1.63 | <0.00638 | *:cellular components* | |
| GO:0016020 | membrane | 54 | 1.86 | <0.00638 | | GO:0005737 |
| GO:0005737 | cytoplasm | 51 | 1.91 | <0.00638 | | GO:0005622 |
| GO:0005634 | nucleus | 86 | 1.95 | <0.00638 | | GO:0005739 |
| GO:0005739 | mitochondrion | 18 | 3.05 | <0.00638 | | GO:0016021 |
| GO:0005654 | nucleoplasm | 9 | 8.25 | <0.00638 | | GO:0016020 |
| | | | | | | GO:0005634 |
| GO:0005509 | calcium ion binding | 27 | 1.84 | 0.04640 | | GO:0005886 |
| GO:0004252 | serine-type endopept | 24 | 2.61 | 0.04640 | | GO:0030286 |
| GO:0003777 | microtubule motor ac | 8 | 3.27 | 0.04060 | *:molecular function* | |
| GO:0036459 | ubiquitinyl hydrolase | 6 | 4.36 | 0.02953 | | GO:0004386 |
| GO:0046872 | metal ion binding | 29 | 1.86 | 0.01624 | | GO:0030515 |
| GO:0005488 | binding | 22 | 2.25 | 0.00902 | | GO:0008270 |
| GO:0005515 | protein binding | 166 | 2.05 | <0.00902 | | GO:0046872 |
| GO:0003677 | DNA binding | 39 | 2.10 | <0.00902 | | GO:0003690 |
| GO:0008270 | zinc ion binding | 57 | 2.30 | <0.00902 | | GO:0003677 |
| GO:0005524 | ATP binding | 64 | 2.34 | <0.00902 | | GO:0003824 |
| GO:0003824 | catalytic activity | 31 | 2.35 | <0.00902 | | GO:0005524 |
| GO:0016887 | ATPase activity | 15 | 2.61 | <0.00902 | | GO:0005515 |
| GO:0003676 | nucleic acid binding | 70 | 2.72 | <0.00902 | | GO:0003676 |
| GO:0000287 | magnesium ion bindir | 7 | 5.36 | <0.00902 | | GO:0016887 |
| | | | | | | GO:0003723 |
| | | | | | | GO:0005488 |
| | | | | | | GO:0003777 |

*partial hard*
*:cellular components*

GO:0000798

| function | U G S count | enrichment | $q$-value |
|---|---|---|---|
| cytoplasm | 98 | 1.37 | 0.03720 |
| membrane | 107 | 1.40 | 0.01240 |
| integral component of | 357 | 1.31 | <0.01240 |
| nucleus | 159 | 1.39 | <0.01240 |
| | | | |
| ATP-dependent RNA l | 11 | 2.46 | 0.04227 |
| double-stranded DNA | 6 | 3.56 | 0.04227 |
| odorant binding | 33 | 2.29 | 0.03444 |
| RNA binding | 39 | 1.76 | 0.00969 |
| ATP binding | 105 | 1.46 | <0.00969 |
| metal ion binding | 58 | 1.51 | <0.00969 |
| protein binding | 309 | 1.51 | <0.00969 |
| nucleic acid binding | 104 | 1.51 | <0.00969 |
| zinc ion binding | 104 | 1.64 | <0.00969 |
| binding | 45 | 1.90 | <0.00969 |
| serine-type endopept: | 46 | 1.99 | <0.00969 |
| | | | |
| membrane | 4 | 22.45 | <0.03900 |
| | | | |
| cell adhesion | 13 | 3.41 | 0.04590 |
| RNA processing | 8 | 3.95 | 0.04590 |
| proteolysis | 34 | 2.92 | 0.04284 |
| signal transduction | 21 | 2.40 | 0.02678 |
| regulation of transcrip | 35 | 2.19 | <0.02678 |

| | | | |
|---|---|---|---|
| microtubule-based m | 9 | 4.42 | <0.02678 |
| mRNA splicing, via spl | 11 | 5.27 | <0.02678 |
| | | | |
| cytoplasm | 39 | 1.85 | 0.02438 |
| intracellular | 25 | 1.98 | 0.02438 |
| mitochondrion | 15 | 3.17 | 0.02438 |
| integral component of | 153 | 1.87 | <0.00780 |
| membrane | 53 | 2.31 | <0.00780 |
| nucleus | 81 | 2.32 | <0.00780 |
| plasma membrane | 31 | 2.36 | <0.00780 |
| dynein complex | 8 | 6.03 | <0.00780 |
| | | | |
| helicase activity | 5 | 5.35 | 0.03634 |
| snoRNA binding | 4 | 7.29 | 0.03262 |
| zinc ion binding | 40 | 2.07 | 0.00707 |
| metal ion binding | 26 | 2.12 | 0.00707 |
| double-stranded DNA | 5 | 9.64 | 0.00707 |
| DNA binding | 34 | 2.32 | <0.00707 |
| catalytic activity | 25 | 2.33 | <0.00707 |
| ATP binding | 52 | 2.40 | <0.00707 |
| protein binding | 159 | 2.49 | <0.00707 |
| nucleic acid binding | 57 | 2.74 | <0.00707 |
| ATPase activity | 15 | 3.32 | <0.00707 |
| RNA binding | 22 | 3.35 | <0.00707 |
| binding | 30 | 3.99 | <0.00707 |
| microtubule motor ac | 8 | 4.27 | <0.00707 |
| | | | |
| nuclear cohesin comp | 1 | INF | <0.03900 |

**Table S7.** Example command lines to generate *discoal* simulations.

AOM        discoal 120 2000 55000 -Pt 100.667293 1006.672930 -Pre 1107.340223 3322.020670 -en 0.000214 0 1.0021

BFM        discoal 138 2000 55000 -Pt 1330.793457 13307.934565 -Pre 14638.728022 43916.184065 -en 0.000161 0 0.

BFS        discoal 162 2000 55000 -Pt 1750.204699 17502.046985 -Pre 19252.251684 57756.755051 -en 0.000038 0 1.

CMS        discoal 182 2000 55000 -Pt 465.266905 4652.669049 -Pre 5117.935954 15353.807861 -en 0.000061 0 1.111

GAS        discoal 112 2000 55000 -Pt 569.780857 5697.808570 -Pre 6267.589427 18802.768280 -en 0.000080 0 0.631

GNS        discoal 62 2000 55000 -Pt 1999.973115 19999.731147 -Pre 21999.704262 65999.112785 -en 0.000820 0 0.9

GWA        discoal 92 2000 55000 -Pt 974.582413 9745.824130 -Pre 10720.406543 32161.219629 -en 0.000242 0 1.001

UGS        discoal 206 2000 55000 -Pt 1165.186611 11651.866111 -Pre 12817.052722 38451.158167 -en 0.000072 0 1.

Location changes by setting the value of $x (between 0 and 1)
To simulate complete sweeps, remove the -Pc flag and values
To simulate hard sweeps, remove the -Pf flag and values
To simulate no sweeps, remove the -Pc, -Pf, -x, -ws, -Pa, and -Pu flags and according values

.85 -en 0.000363 0 1.003592 -en 0.000439 0 1.003717 -en 0.000517 0 1.020643 -en 0.000598 0 1.024216 -en 0.000680 0 1.
.985949 -en 0.000216 0 0.983492 -en 0.000271 0 1.000000 -en 0.000328 0 0.999114 -en 0.000385 0 1.000000 -en 0.00044
.001158 -en 0.000077 0 1.004693 -en 0.000117 0 1.017850 -en 0.000157 0 1.019335 -en 0.000198 0 1.022229 -en 0.00024
.333 -en 0.000096 0 2.040230 -en 0.000160 0 2.927333 -en 0.000252 0 3.603759 -en 0.000368 0 3.724538 -en 0.000489 0 3
.586 -en 0.000132 0 0.589447 -en 0.000181 0 0.159569 -en 0.000195 0 0.159078 -en 0.000209 0 0.154646 -en 0.000222 0 (
.92861 -en 0.001110 0 0.794064 -en 0.001350 0 0.540221 -en 0.001520 0 0.490645 -en 0.001679 0 0.473441 -en 0.001838
.700 -en 0.000367 0 1.007686 -en 0.001640 0 1.007342 -en 0.002131 0 1.007686 -en 0.002480 0 1.008099 -en 0.003237 0 (
.000968 -en 0.000096 0 1.008257 -en 0.000121 0 1.008772 -en 0.000146 0 1.022998 -en 0.000172 0 1.007552 -en 0.00019

024809 -en 0.000764 0 1.037077 -en 0.000851 0 1.040212 -en 0.000939 0 1.043685 -en 0.001029 0 1.054121 -en 0.00112
4 0 1.077979 -en 0.000508 0 1.071814 -en 0.000573 0 1.024200 -en 0.000636 0 1.049526 -en 0.000702 0 1.070901 -en 0.00
0 0 1.025899 -en 0.000282 0 1.030126 -en 0.000326 0 1.030824 -en 0.000369 0 1.031031 -en 0.000459 0 1.031171 -en 0.00
3.778291 -en 0.000613 0 3.793999 -en 0.000739 0 3.801097 -en 0.000867 0 3.813393 -en 0.000997 0 3.819256 -en 0.00112
0.153297 -en 0.000236 0 0.151153 -en 0.000250 0 0.149826 -en 0.000278 0 0.149120 -en 0.000511 0 0.149826 -en 0.00053
0 0.467565 -en 0.002002 0 0.463145 -en 0.002170 0 0.461279 -en 0.002344 0 0.456089 -en 0.002523 0 0.453183 -en 0.002
0.997880 -en 0.003438 0 0.560152 -en 0.003554 0 0.530789 -en 0.003667 0 0.530786 -en 0.003784 0 0.530789 -en 0.00390
7 0 1.003068 -en 0.000223 0 1.001495 -en 0.000249 0 1.000662 -en 0.000275 0 0.997039 -en 0.000302 0 0.997529 -en 0.00

2 0 1.074898 -en 0.001219 0 1.079116 -en 0.001318 0 1.085179 -en 0.001419 0 1.089208 -en 0.001523 0 1.089378 -en 0.00
00770 0 1.020093 -en 0.000836 0 0.974589 -en 0.000900 0 0.893579 -en 0.000959 0 0.829158 -en 0.001015 0 0.741725 -en
00891 0 1.030126 -en 0.000943 0 1.027106 -en 0.000995 0 1.019246 -en 0.001047 0 1.019335 -en 0.001100 0 1.019086 -en
28 0 3.828034 -en 0.001261 0 3.836271 -en 0.001396 0 3.850718 -en 0.001534 0 3.864462 -en 0.001673 0 3.866261 -en 0.0
30 0 0.150585 -en 0.000550 0 0.158882 -en 0.000572 0 0.165277 -en 0.000595 0 0.170755 -en 0.000620 0 0.504559 -en 0.0
2708 0 0.451860 -en 0.002900 0 0.450422 -en 0.003099 0 0.448048 -en 0.003307 0 0.446177 -en 0.003747 0 0.445082 -en
04 0 0.530786 -en 0.004027 0 0.528428 -en 0.004154 0 0.526746 -en 0.004285 0 0.526125 -en 0.004703 0 0.524966 -en 0.0
00328 0 0.995950 -en 0.000382 0 0.994539 -en 0.000410 0 0.995950 -en 0.000437 0 0.997039 -en 0.000465 0 1.000000 -en

)1628 0 1.090078 -en 0.001846 0 1.095578 -en 0.001959 0 1.095843 -en 0.003823 0 1.095578 -en 0.004141 0 1.089208 -en
ı 0.001066 0 0.697406 -en 0.001115 0 0.673163 -en 0.001163 0 0.648442 -en 0.001210 0 0.625999 -en 0.001256 0 0.61677
ı 0.001154 0 1.019246 -en 0.001209 0 1.020601 -en 0.001265 0 1.018926 -en 0.001321 0 1.013910 -en 0.001378 0 1.00468
)01814 0 3.870850 -en 0.002102 0 3.876694 -en 0.002249 0 3.879188 -en 0.002398 0 3.891219 -en 0.002702 0 3.891609 -e
)00694 0 0.617331 -en 0.000787 0 0.670013 -en 0.000890 0 0.682974 -en 0.000998 0 0.694737 -en 0.001111 0 0.696173 -e
0.004229 0 0.433300 -en 0.004481 0 0.167095 -en 0.004583 0 0.167041 -en 0.004690 0 0.166713 -en 0.004802 0 0.165622
)04851 0 0.524897 -en 0.005004 0 0.524506 -en 0.005498 0 0.523930 -en 0.005857 0 0.523704 -en 0.006047 0 0.523703 -e
ı 0.000494 0 0.999703 -en 0.000523 0 0.997529 -en 0.000552 0 1.000968 -en 0.000581 0 1.003490 -en 0.000611 0 1.00455

1 0.004305 0 1.085229 -en 0.004473 0 1.064777 -en 0.004641 0 1.022083 -en 0.004807 0 0.971303 -en 0.004969 0 0.71761

72 -en 0.001303 0 0.612164 -en 0.001349 0 0.609098 -en 0.001397 0 0.606156 -en 0.001444 0 0.605458 -en 0.001493 0 0.6

33 -en 0.001435 0 1.000118 -en 0.001493 0 0.985278 -en 0.001551 0 0.967523 -en 0.001608 0 0.621680 -en 0.001646 0 0.5

en 0.002856 0 3.898662 -en 0.003014 0 3.903107 -en 0.003334 0 3.906573 -en 0.003498 0 3.918087 -en 0.004177 0 3.9235

en 0.001227 0 0.695425 -en 0.001346 0 0.670013 -en 0.001463 0 0.665223 -en 0.001583 0 0.628336 -en 0.001700 0 0.5947

2 -en 0.004920 0 0.165268 -en 0.005044 0 0.164789 -en 0.005175 0 0.164082 -en 0.005313 0 0.163800 -en 0.005459 0 0.16

en 0.006450 0 0.523432 -en 0.006886 0 0.522467 -en 0.007118 0 0.518847 -en 0.007358 0 0.518125 -en 0.007608 0 0.5151

54 -en 0.000671 0 1.006577 -en 0.000702 0 1.008257 -en 0.000734 0 1.008763 -en 0.000765 0 1.012032 -en 0.000797 0 1.0

3 -en 0.005091 0 0.537087 -en 0.005185 0 0.499553 -en 0.005275 0 0.485986 -en 0.005553 0 0.481404 -en 0.005749 0 0.4

03039 -en 0.001543 0 0.602428 -en 0.001593 0 0.597894 -en 0.001644 0 0.597796 -en 0.001695 0 0.591886 -en 0.001747

99478 -en 0.001683 0 0.583576 -en 0.001719 0 0.576138 -en 0.001756 0 0.564006 -en 0.001792 0 0.559137 -en 0.001829

46 -en 0.004710 0 3.933192 -en 0.004894 0 3.941164 -en 0.006667 0 3.944081 -en 0.006879 0 3.941164 -en 0.007093 0 3.

45 -en 0.001813 0 0.551675 -en 0.001921 0 0.449593 -en 0.002011 0 0.182750 -en 0.002049 0 0.176691 -en 0.002087 0 0.

3448 -en 0.005614 0 0.163443 -en 0.005778 0 0.163309 -en 0.005954 0 0.163127 -en 0.006141 0 0.162466 -en 0.006342 0

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490114 -en 0.009340 0 0.468610 -en 0.009656 0 0.438019 -en 0.009967 0 0.417032 -en 0.010280 0 0.406419 -en 0.01060

0 1.023465 -en 0.000999 0 1.024238 -en 0.001035 0 1.026880 -en 0.001070 0 1.027391 -en 0.001107 0 1.029008 -en 0.00

0 0.488293 -en 0.007643 0 0.557396 -en 0.007838 0 0.562350 -en 0.008042 0 0.565078 -en 0.008255 0 0.569917 -en 0.00
2202 0 0.588174 -en 0.002264 0 0.586833 -en 0.002327 0 0.586283 -en 0.002391 0 0.579687 -en 0.002456 0 0.575413 -en
2226 0 0.550215 -en 0.002751 0 0.550213 -en 0.004234 0 0.550215 -en 0.004410 0 0.549391 -en 0.004502 0 0.549190 -en
9 0 3.827356 -en 0.008671 0 3.789089 -en 0.008904 0 3.782912 -en 0.009140 0 3.771942 -en 0.009380 0 3.733972 -en 0.0
9 0 0.171531 -en 0.002333 0 0.171340 -en 0.002378 0 0.171091 -en 0.002425 0 0.171054 -en 0.002473 0 0.170923 -en 0.0
904 0 0.159987 -en 0.009052 0 0.132045 -en 0.010355 0 0.129493 -en 0.010895 0 0.116267 -en 0.011449 0 0.107984 -en
3 0 0.389248 -en 0.010930 0 0.379522 -en 0.011268 0 0.370162 -en 0.011619 0 0.365981 -en 0.011988 0 0.365069 -en 0.0
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