

501 **SUPPLEMENTARY MATERIAL**

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503 **Supplemental Table 1. Characteristics of within-population balancing selection versus**
 504 **local adaptation via SVS.**

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Feature	Balanced local polymorphism	Local adaptation (population divergence)	Notes
<i>Spatial scale of environmental heterogeneity (patch size)</i>	Fine patches (patch size << geographic range of population)	Coarse patches or clinal variation	“Coarse” patches are a simplified view of situations where relative contribution of “fine” patches to local environment differs.
<i>Relative gene flow between patches</i>	High	Low-moderate	Assortative mating, short-range dispersal, and oviposition/feeding preference can reduce gene flow and promote balanced local polymorphisms (and, if strong enough, promote host race formation). [1-3]
<i>Observed fitness effects between patches</i>	Antagonistic pleiotropy	Antagonistic pleiotropy; conditional neutrality	Conditional neutrality is not expected to maintain long-term polymorphism, but is often observed in local adaptation. Undetected antagonistic pleiotropy could be due to methodological biases/limitations, or result from low gene flow between populations. [4]
<i>Type of selection within populations on contextually beneficial alleles</i>	Antagonistic selection	Positive directional selection	Assumes a classical local adaptation model in which one allele sweeps to high frequency; local adaptation can also proceed through shifts in allele frequencies across populations.
<i>Relative speed of a selective sweep</i>	Slow	Fast	Sweeps are slower for antagonistic selection than other forms of balancing selection, but allelic dominance reversals across patches or co-occurring frequency dependent selection reduce the magnitude of this effect. [5]

<i>Polymorphism at causative sites in contextually beneficial alleles</i>	Elevated within populations; elevated at species level	Reduced within populations; elevated at species level	Fine and coarse-grained spatially variable selection maintain polymorphism over different scales (within vs. among populations).
<i>Population divergence at causative sites in contextually beneficial alleles</i>	Reduced	Elevated	Selection for standing variation can lead to <i>reduced</i> inter-population divergence between populations inhabiting similar habitats and <i>elevated</i> divergence between populations inhabiting dissimilar habitats.

507 **Supplemental Table 2. Population and quantitative genetic methods to detect balancing**
 508 **selection driven by spatial variation.** Note that other forms of balancing selection may leave
 509 similar signatures when looking within single populations.

Temporal Scale [6]	Nature of evidence for adaptation [with key references]	Application to balanced local polymorphism	Application to locally adaptive divergence	Notes and/or explanations
Current Generation	Association of genotype with fitness or fitness-related traits [7-11]	QTL mapping, genome-wide association studies, evolve-and-resequence experiments	QTL mapping, genome-wide association studies, evolve-and-resequence experiments	Large mapping populations incorporate information from many recombination events, increasing mapping resolution.
	Association of genotype with habitat characteristics in the field [12]	Correlation of genotype with habitat for individuals <i>within</i> populations	Correlation of allele frequencies with habitat characteristics across many populations	Allele frequency differences could be maintained by many forces, e.g. differential insect preference or performance on different plants, or plant performance when exposed to different insect communities.
Recent Past	Interpopulation divergence [13-16]	$\downarrow (F_{ST})$	$\uparrow (F_{ST})$ between populations in divergent patches, but $\downarrow (F_{ST})$ following parallel adaptation to similar patches from standing genetic variation	Forces favoring within-population polymorphism or alternative alleles in different populations slow or accelerate divergence at those loci, respectively, relative to genetic drift. Hierarchical outlier analysis can identify alleles under SVS in a background of neutral population genetic structure.
	Linkage disequilibrium (LD) [5,17]	Each favored variant falls within	Locally favored variants will be within	Haplotype-based tests are powerful for detecting rapid partial sweeps, but unclear

		extended, intermediate frequency haplotypes	extended, high frequency haplotypes	whether many of the slow sweeps under spatially varying selection leave detectable genomic signatures.
	Allele frequency spectrum [18,19]	Excess of intermediate frequency alleles (Tajima's D)	Excess of rare alleles (Tajima's D)	Uncommon variants linked to selected haplotype(s) rise to intermediate frequency when multiple haplotypes are favored in a population (but see above). Demographic changes and population subdivision strongly affect Tajima's D.
Distant Past	Polymorphism (π) vs. divergence (d) [20-22]	Elevated π/d (HKA test), excess non-synonymous polymorphism (MK test)	Reduced π/d (HKA test), excess non-synonymous divergence (MK test)	Careful thought is required to identify the appropriate scale to estimate polymorphism and divergence (e.g. within or among populations or species). Using outgroups to polarize changes is desired.
	Trans-species polymorphism [23]	Small haplotypes shared between species		Various forms of balancing selection can preserve polymorphism for long periods, but recombination and mutation erode this pattern at neutral sites linked to the causal variants.

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512 **Supplemental Table 3: Distribution records for *Scaptomyza flava* (including synonyms *S.***
 513 ***flaveola*, *S. apicalis*, and *S. montana*).**

Country	Subnational area or island	<i>S. flava</i> reference
United States	Alaska	[2]
	New York	[2]
	Connecticut	[2]
	Massachusetts	Personal collection, [2]
	New York	[2]
	Indiana	[2]
	Maryland	[2]
	Washington, DC	[2]
	California	[2]
	Idaho	[2]
	Oregon	[2]
	Virginia	[2]
	Arizona	Personal collection
Canada	Nova Scotia	[2]
Russia	Far East	[8]
	Eastern Siberia	[8]
	Western Siberia	[8]
	European	[8]
China	Xinjiang	[9]
Portugal	Mainland	[11]
	Azores	[2]
	Madeira Islands	[2]

Spain	Mainland	[11]
	Canary Islands	[2]
Czech Republic		[4]
Slovakia		[4]
United Kingdom		[10]
Ireland		[10]
Germany		[10]
Italy		[10]
Netherlands		[10]
Belgium		[10]
Finland		[3]
Norway		[1]
Sweden		[1]
Denmark		[1]
Turkey		[1]
Austria		[1]
Switzerland		[1]
Estonia		[1]
Latvia		[1]
Lithuania		[1]
Poland		[1]
France	mainland	[11]
	Corsica	[11]
Greece	Mainland	[11]
	Crete	[11]

Ukraine		[11]
Bulgaria		[11]
Romania		[11]
Bosnia and Herzegovina		[11]
Slovenia		[11]
Serbia		[11]
Macedonia		[11]
Croatia		[11]
Uzbekistan		[8]
Mongolia		[6]
New Zealand		[5]
Iran		[7]
Japan		[8]

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