Consequences of single-locus and tightly linked genomic architectures for evolutionary responses to environmental change

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Running title: Genomic architecture shapes evolutionary responses

Abstract

Genetic and genomic architectures of traits under selection are key factors influencing evolutionary responses. Yet, knowledge of their impacts has been limited by a widespread assumption that most traits are controlled by unlinked polygenic architectures. Recent advances in genome sequencing and eco-evolutionary modelling are unlocking the potential for integrating genomic information into predictions of population responses to environmental change. Using eco-genetic simulations, we demonstrate that hypothetical single-locus control of a life history trait produces highly variable and unpredictable harvesting-induced evolution relative to the classically applied multi-locus model. Single-locus control of complex traits is thought to be uncommon, yet blocks of linked genes, such as those associated with some types of structural genomic variation, have emerged as taxonomically widespread phenomena. Inheritance of linked architectures resembles that of single loci, thus enabling single-locus-like modeling of polygenic adaptation. Yet, the number of loci, their effect sizes, and the degree of linkage among them all occur along a continuum. We review how linked architectures are often associated, directly or indirectly, with traits expected to be under selection from anthropogenic stressors and are likely to play a large role in adaptation to environmental disturbance. We suggest using single-locus models to explore evolutionary extremes and uncertainties when the trait architecture is unknown, refining parameters as genomic information becomes available, and explicitly incorporating linkage among loci when possible. We discuss some challenges involved in modelling the evolutionary dynamics of linked genomic architectures and implementing such knowledge in the conservation and management of natural populations.

Keywords: climate change, evolutionary simulation, genetic architecture, linkage disequilibrium, recombination rate, structural genomic variation

Eco-evolutionary responses hinge on genetic and genomic architecture

Predicting the responses of populations and species to anthropogenic disturbance is a major challenge, and one that requires urgent attention given the current climate and biodiversity crises (IPCC 2018; IPBES 2019). Advances in second- (high throughput) and third- (long read) generation sequencing have produced a wealth of sequence and structural genomic data on non-model organisms. These data have great potential to inform eco-evolutionary models of the responses of natural populations to a variety of selection pressures (Hoffmann *et al.* 2015; Bay *et al.* 2017a; Coulson *et al.* 2017). Such models can inform current management strategies and facilitate human societal adaptation to future environmental conditions and associated ecosystem structures.

Key parameters influencing evolutionary responses are the genetic and genomic architectures underlying adaptive traits. Genetic architecture broadly refers to how a trait is controlled by genes and interactions among alleles (e.g., number and effect sizes of contributing loci, dominance, epistasis, pleiotropy), while genomic architecture includes structural arrangement (e.g., inversions, fusions, translocations, duplications), position, and linkage among loci. Both types of architecture contribute to the inheritance models for genes underlying adaptive traits that are used in evolutionary predictions.

Here, we discuss some effects of genetic (the number of loci and their effect sizes) and genomic (the degree of linkage among loci) architectures on predictions of evolutionary responses to environmental disturbance. Single or unlinked loci have received comparatively more attention than linked genomic architectures in this regard (Bay *et al.* 2017a; Kardos & Luikart 2019). We demonstrate that hypothetical single locus control of a life history trait under harvesting-induced selection generates a more variable evolutionary response compared to an unlinked polygenic scenario. We then suggest that linked polygenic architectures resemble those of single large-effect loci, yet exist along a continuum of linkage disequilibrium, and are likely to play a large role in adaptation to rapid environmental change. We show that linked architectures underlie diverse traits in natural populations that are directly or indirectly under environmental selection. Finally,

81 we discuss some barriers to modelling such architectures and challenges they present to
82 conservation and management. More broadly, we aim to promote the integration of
83 genomic data into eco-evolutionary modelling of responses to environmental change.
84
85 *Large-effect loci alter evolutionary predictions compared to traditional multi-locus*
86 *models*
87
88 Considering genetic architecture, the degree to which a trait is controlled primarily by a
89 single locus or multiple loci will influence its evolution in response to environmental
90 stressors. Traditional evolutionary models have focused on the fixation dynamics of
91 single-locus traits suddenly exposed to selection (Orr & Unckless 2014). As single-locus
92 control of complex traits has been considered rare (Feder & Walser 2005), eco-
93 evolutionary models of complex non-model organisms often incorporate a standard
94 inheritance model of 10 or 20 unlinked loci (e.g., Kuparinen & Hutchings 2012). Multi-
95 locus (e.g., 100+ loci) models based on genomic single nucleotide polymorphism (SNP)
96 data have also been employed more recently to predict the capacity of a population to
97 evolve in pace with global climate change (Bay *et al.* 2017a, 2018). Bay *et al.* (2017b)
98 described a potential framework for genomic predictions of adaptive responses to
99 environmental change, termed 'evolutionary response architectures', but focused on
100 unlinked polygenic control of climate-associated traits.
101
102 The assumption that single genetic variants accounting for large amounts of phenotypic
103 variation are rare is being challenged as more refined statistical genomics enable their
104 discovery (Hoban *et al.* 2016). Large-effect loci have been documented in plants
105 (Kivimäki *et al.* 2007; Baxter *et al.* 2010), mammals (Johnston *et al.* 2013; Kardos *et al.*
106 2015; Jones *et al.* 2018; Barrett *et al.* 2019), birds (Toews *et al.* 2019; Merritt *et al.*
107 2020), and fishes (Colosimo *et al.* 2004; Lampert *et al.* 2010; Barson *et al.* 2015;
108 Thompson *et al.* 2019). The implications of these variants for eco-evolutionary model
109 predictions can be severe. For example, after the discovery that the *vgll3* gene is
110 responsible for 40% of the variation in age at maturity in Atlantic salmon (*Salmo salar*)
111 (Barson *et al.* 2015), Kuparinen and Hutchings (2017) demonstrated that hypothetical

single-locus control of this key, sexually dimorphic life-history trait generates divergent and disruptive fisheries-induced evolution relative to that predicted by the classically applied, commonly assumed multi-locus model.

Single-locus architecture generates divergent evolutionary responses to harvesting

We revisited this model to compare hypothetical single- and multi-locus architectures, but without dimorphic trait expression, to assess whether genetic architecture affected trait evolution in a more general scenario absent of sexual dimorphism. To this end, we took simple averages of the sex-specific probabilities for the male and female age at maturity. By doing this, a male and a female carrying the same single-locus genotype have the same probabilities to mature at the ages of 1SW, 2SW and 3 SW. We simulated 10 independent evolutionary trajectories for both the single-locus and the multi-locus control scenarios and tracked the average age at maturity for each simulation time step. The simulations involved three phases: i) pristine conditions in the absence of fishing (500 years, the first 400 of which were discarded as burn-in), ii) exposure to selective fishing mortality at the rate of 0.2, and iii) recovery in the absence of fishing. The detailed model description and parameter values are reported in Kuparinen & Hutchings (2017).

Despite dimorphism being absent, the simulations demonstrate that single-locus control of age at maturity generates increased variability in this trait compared to the multi-locus scenario and that the response to, and recovery from, fishing are also highly varied (Figure 1). In the single locus scenario, oscillations driven by chaotic dynamics are evident under pristine conditions, reduced at varying rates under fishing pressure, and markedly return in only three out of ten simulations (Figure 1a,c). In contrast, the multi-locus scenario does not generate chaotic dynamics and exhibits little variability both within and between simulations (Figure 1b,d). Therefore, single locus control of age at maturity with and without sexually dimorphic expression results in highly unpredictable evolutionary and ecological responses to fishing-induced selection on this trait, relative to the commonly assumed multi-locus control.

143

144 This result is consistent with recent simulations demonstrating increased variability in
145 population viability under rapid directional environmental change when the trait under
146 selection is under single-locus rather than multi-locus control (Kardos & Luikart 2019). It
147 further suggests that recovery following relaxation of selection is also highly variable.

148

149 *Inheritance of linked polygenic architectures resembles that of single loci*

150

151 Particularly for complex traits, such as those contributing to growth, behaviour, or
152 environmental responses, polygenic control might indeed be the norm (Savolainen *et al.*
153 2013; Palumbi *et al.* 2014; Bay *et al.* 2017a). Yet, considering genomic architecture,
154 blocks of tightly linked putatively adaptive genes that undergo reduced or no
155 recombination are taxonomically widespread (Nosil *et al.* 2009; Rogers *et al.* 2011;
156 Yeaman 2013; Wellenreuther & Bernatchez 2018).

157

158 There are several mechanisms by which linked clusters might evolve in response to
159 selection, but all are characterized by a reduction in recombination (Yeaman 2013). This
160 is because when linkage captures an advantageous allelic combination, selection will
161 favour a reduced recombination rate in that region to avoid splitting up complementary
162 alleles (Charlesworth & Charlesworth 1979; Kirkpatrick & Barton 2006; Bürger &
163 Akerman 2011; Yeaman & Whitlock 2011). Low recombination rates can be achieved by
164 genic modifiers that decrease the frequency of crossovers during meiosis or genomic
165 rearrangements that alter gene order, suppress recombination, and/or generate unbalanced
166 gametes in heterozygotes (Figure 2; Butlin 2005; Ortiz-Barrientos *et al.* 2016).
167 Recombination rate is also negatively correlated with epistasis, chromosome length, and
168 proximity among loci (Kong *et al.* 2002; Butlin 2005). Further, sequence content can
169 have both positive (CpG content) and negative (GC, polyA/polyT, and heterochomatin
170 content) effects on recombination rate (Kong *et al.* 2002). The lower the rate of
171 recombination, the more the inheritance pattern of a genomic region containing multiple
172 loci resembles that of a single locus, such that complete linkage among genes would
173 result in their co-inheritance (Figure 3).

174

175 *Linked polygenic architectures are ubiquitous and exist along a continuum of linkage*
176 *disequilibrium*

177

178 Linked regions are often identified in population genomic studies as 'genomic islands of
179 divergence' (regions that exhibit greater differentiation than expected under neutrality;
180 Wu 2001), although the degree of linkage varies depending on the mechanism of
181 recombination suppression (Figure 2). For example, genic modifiers might only partially
182 reduce recombination, leading to low or moderate levels of linkage disequilibrium (LD;
183 non-random association of alleles at different loci)(Butlin 2005).

184

185 In contrast, extreme cases of tightly linked co-adapted gene complexes associated with
186 discrete complex phenotypes, known as supergenes, underlie key life-history traits in a
187 variety of species (Schwander *et al.* 2014). Supergenes are often associated with
188 structural genomic variation, which underlies complex phenotypes and adaptive
189 processes in a wide variety of non-model taxa (Mérot *et al.* in review; Wellenreuther *et*
190 *al.* 2019). There is emerging evidence that structural variants might comprise the most
191 important source of genetic variation in natural populations, as they have been found to
192 account for several times more genomic variation than SNPs (e.g., 3x in the Australasian
193 snapper [*Chrysophrys auratus*; Catanach *et al.* 2019], 12x in *Homo sapiens* [Pang *et al.*
194 2010]).

195

196 One of the most well studied types of structural variant is the chromosomal inversion
197 (Sturtevant 1921; Wellenreuther *et al.* 2019). Inversions prevent recombination within the
198 inverted region by displacing crossovers away from breakpoints during meiosis (at least
199 in *Diptera* flies) or by producing lethal meiotic products (if the inversion does not include
200 the centromere) or inviable gametes (if the inversion spans the centromere) in
201 heterokaryotypes, resulting in the selective recovery of non-recombinant chromosomes
202 (Reiseberg 2001; Hoffmann & Rieseberg 2008; Wellenreuther & Bernatchez 2018).

203

204 Other types of structural variation, such as chromosomal fusions and fissions,
205 translocations, and copy number variants (CNVs), can also generate unbalanced gametes
206 (Rieseberg 2001), which is expected to have similar implications for recombination rate
207 reduction. Chromosomal fusions reduce recombination to a lesser extent than inversions,
208 but to varying degrees in both heterozygotes and fused homozygotes (Bidau *et al.* 2001;
209 Guerrero & Kirkpatrick 2014). There is also at least one example of a complex CNV
210 maintaining linkage among candidate genes associated with multiple traits, effectively
211 acting as a supergene (Tigano *et al.* 2018). While the precise mechanisms for reducing
212 recombination are not yet clear for many types of structural variation, the field is poised
213 for major advances (Mérot *et al.* in review).
214
215 *Linked architectures play a large role in adaptation to rapid change*
216
217 Linked architectures are hypothesized to facilitate rapid adaptation by enabling
218 inheritance of co-adapted gene complexes. Instead of accumulating beneficial alleles over
219 multiple generations, they come as a package that has the potential to spread rapidly
220 through a population, similar to a single large-effect gene (Kirkpatrick & Barrett 2015).
221 Therefore, while the extent of recombination in linkage blocks can vary, a linked
222 genomic architecture would enable single-locus-like modeling of polygenic adaptation.
223 Their prevalence, especially the rising ubiquity of structural variation, necessitates a
224 reassessment of common assumptions regarding the degree to which genes contributing
225 to a polygenic trait are likely to be physically linked and/or experience reduced
226 recombination. Next, we seek to highlight the broad potential of modelling linked
227 architectures for the purpose of predicting responses of natural populations to
228 environmental disturbance.
229

230 **Linked genomic architectures underlie diverse traits in natural populations that are**
231 **directly or indirectly under environmental selection**
232
233 In recent years, linked genomic architectures have been associated with a variety of
234 adaptive traits in natural populations (Table 1). While inversions appear to be the most

235 commonly studied (Wellenreuther & Bernatchez 2018; Wellenreuther *et al.* 2019),
236 chromosomal fusions (Wellband *et al.* 2019) and complex architectures involving
237 multiple rearrangements (Tigano *et al.* 2018; Pearse *et al.* 2019) are also associated,
238 directly or indirectly, with traits relevant for adaptation. In some cases, SNPs located in
239 proximity to one another are found to be in LD and the structural architecture is yet to be
240 determined (e.g., Micheletti *et al.* 2018). Considering that the cataloguing of structural
241 genomic variation is still in its infancy and that our understanding of recombination rate
242 variation is lacking (Mérot *et al.* in review), we adopt an inclusive approach regarding the
243 examples discussed.
244
245 *Linked architectures are favoured by selection under gene flow*
246
247 Theoretical work has implicated the genetic and genomic architecture of adaptive traits as
248 the key element in determining whether they will be lost under gene flow (Bürger &
249 Akerman 2011; Yeaman & Whitlock 2011; Yeaman 2013; Aeschbacher & Bürger 2014;
250 Akerman & Bürger 2014). Alleles with large effect sizes are less likely to be
251 overwhelmed by gene flow (Yeaman & Otto 2011), as are tightly linked polygenic
252 architectures because they effectively act as a single large-effect locus (Griswold 2006;
253 Yeaman & Otto 2011). Gene flow increases the risk of breaking up co-adapted alleles,
254 thereby selecting for reduced recombination and increased linkage (Nosil *et al.* 2009;
255 Tigano & Friesen 2016).
256
257 The evolution of linked architectures under gene flow might explain why they appear to
258 be common in species with high dispersal capabilities: flying insects, birds, and fishes
259 (Table 1; Wellenreuther & Bernatchez 2018). Many examples of extremely tight linkage
260 derive from systems in which closely related species or ecotypes are living in sympatry
261 (Nosil *et al.* 2009; Hooper 2016). Yet, high gene flow is pervasive in the natural world,
262 including many plants with high seed dispersal and marine organisms with pelagic early
263 life stages. Therefore, linked architectures are likely common.
264
265 *Linked architectures are often directly associated with environmental adaptation*

Linked architectures associated with adaptation to local environmental variables seem particularly common among flies and fishes (Table 1; Wellenreuther & Bernatchez 2018). Flies in the genus *Drosophila* provide numerous examples of inversions associated with environmental adaptation, including those exhibiting latitudinal (Krimbas & Powell 1992; Anderson *et al.* 2005; Rane *et al.* 2015; Fuller *et al.* 2016, 2017; Kapun & Fabian 2016; Kapun & Flatt 2019) and altitudinal (Kapun & Flatt 2019) clines, as well as adaptation to a desert environment (possibly through the host plant; Guillén & Ruiz 2012). Of particular interest from a human health perspective, environmentally structured inversion polymorphisms are common among *Anopheles* spp. mosquitos, potentially enhancing the adaptability and vector potency of these primary malaria vectors (Ayala *et al.* 2014, 2017). Inversions in *Anopheles* spp. vary in karyotype frequencies across latitudinal clines and between mountain forests and lowland savannahs (Ayala *et al.* 2017), and are associated with aridity tolerance.

Inversions and blocks of differentiation (which may or may not be associated with inversions) appear to underlie adaptation to salinity (Jones *et al.* 2012; Berg *et al.* 2015) and vary in frequency across latitudinal clines in marine fishes, suggesting an association with temperature or growing season length (Pettersson *et al.* 2019; Therkildsen *et al.* 2019; Kess *et al.* 2020). Chromosomal translocations and fusions are common among salmonids (Phillips 2005). Their adaptive significance, if any, is not generally known, although a fusion in Atlantic salmon (Ssa08/Ssa29) is associated with summer precipitation in a Canadian river system (Wellband *et al.* 2019).

While we have focused on adaptation to abiotic environmental variables, traits controlled by linked architectures can also be associated with the biotic environment. For example, cryptic colouration in timena stick insects (Lindtke *et al.* 2017; Lucek *et al.* 2019) and mimicry patterns in butterflies (Joron *et al.* 2013; Nishikawa *et al.* 2015), associated with a large haploblock and inversions, respectively, are under selection via local host plants and predators associated with particular environments. Changes in these environments

296 can alter camouflage substrates and predator distributions. Adaptation will therefore
297 depend partly on the evolutionary dynamics of the linked regions.
298
299 *Linked architectures are also indirectly associated with environmental adaptation*
300
301 Architectures that link genes controlling several types of co-adapted traits can result in
302 indirect selection on traits associated with environmental adaptation. The inversions in
303 *Anopheles* spp. associated with differences in aridity tolerance (Cheng *et al.* 2018) are
304 also associated with morphology and behaviour (reviewed by Ayala *et al.* 2014).
305 Inversions underlie alternative reproductive phenotypes in some birds (Thomas *et al.*
306 2008; Horton *et al.* 2014; Küpper *et al.* 2015; Zinzow-Kramer *et al.* 2015),
307 simultaneously controlling morphological (e.g., plumage colouration), behavioural (e.g.,
308 mating tactic), and life history (e.g., maturation, growth rate) traits. Common murres
309 (*Uria aalge*) have a complex CNV maintaining linkage among genes associated with
310 plumage colouration and thermal tolerance despite random mating (Tigano *et al.* 2018).
311
312 Alternate behavioural or life history strategies often impose different environmental
313 selection pressures. Fish populations that migrate between freshwater and saltwater for
314 reproduction and feeding require different temperature and salinity adaptations compared
315 to resident populations that don't migrate. Consequently, linked architectures in marine
316 and freshwater fishes are associated with coexisting migratory ecotypes experiencing
317 different environments (Table 1; Pearse *et al.* 2014, 2019; Berg *et al.* 2016; Kirubakaran
318 *et al.* 2016; Arostegui *et al.* 2019; Kess *et al.* 2019). For example, a double inversion in
319 steelhead/rainbow trout (*Oncorhynchus mykiss*) varies in frequency between anadromous
320 and resident populations, as well as between fluvial and adfluvial populations, and
321 exhibits latitudinal- and temperature-associated frequency clines (Pearse *et al.* 2014,
322 2019; Arostegui *et al.* 2019).
323
324 Variation in reproductive timing can require adaptations to different environmental
325 conditions, such as different temperatures experienced during early life (Oomen &
326 Hutchings 2015, 2016), which could favour architectures that link genes associated with

environmental and life history traits. An inversion in Atlantic herring (*Clupea harengus*) is associated with both temperature and timing of reproduction (Fuentes-Pardo *et al.* 2019; Pettersson *et al.* 2019), whereas linked regions in Chinook salmon (*O. tshawytscha*; Narum *et al.* 2018) and steelhead (Micheletti *et al.* 2018) are associated with the timing of arrival to spawning grounds.

Many social traits in insects, birds, fishes, and plants are controlled by linked architectures due to bidirectional influences between social behaviour and genome architecture (reviewed by Rubenstein *et al.* 2019). For example, a supergene containing multiple chromosomal rearrangements underlies several social traits in the fire ant (*Solenopsis invicta*; Huang *et al.* 2018). The connection between social traits and linked architectures has broad relevance for predicting responses to environmental change, as sociality itself is often under environmental selection. For example, thermal stress and resource scarcity select for more or less sociality in different species and contexts (Kao *et al.* submitted; Doering *et al.* 2018). Further, social traits are often correlated with phenotypes that might be under selection from anthropogenic stressors such as climate change and harvesting (e.g. alternative mating tactics and growth rate in swordtail fish [*Xiphophorus* spp.; Lampert *et al.* 2010]).

Theory predicts that supergenes are also likely to arise when there is coevolution between social traits and dispersal, because dispersal will be selected against in benevolent individuals so that they tend to interact with relatives and selected for in selfish individuals so that they tend to interact with nonrelatives (Mullon *et al.* 2018; Rubenstein *et al.* 2019). Therefore, linkage between genes for dispersal traits (e.g., locomotion, physiology) and social behaviour is expected to evolve under a variety of circumstances (Rubenstein *et al.* 2019). As dispersal is one of the primary mechanisms of organismal responses to environmental change, control by linked architectures will likely alter predictions of responses to disturbance in a wide array of taxa.

Therefore, selection on diverse traits could indirectly impose selection on traits associated with environmental adaptation and incorporating linkage when modelling environmental responses has broad taxonomic utility.

Flexible eco-genetic models can reflect a diversity of genomic architectures

The best modelling strategy will depend on what is known regarding the genomic trait architecture. For most traits, the precise architecture is not known and is often estimated to consist of between 10 and 100 unlinked loci of equal effects (e.g., Kuparinen & Hutchings 2012). Given the rising prevalence of major effect loci and tightly linked architectures, exploring both extremes – single locus, representing both major effect and tightly linked loci, and highly polygenic, unlinked loci – is warranted. In reality, an intermediate architecture is likely. Yet, the output of these extreme scenarios will be informative about the range and distribution of possible outcomes and the sensitivity of the model to the genomic architecture in a particular case (e.g., life history or selection regime). As genomic information becomes available, more precise estimates of the number of loci, their effect sizes, and the degree of linkage among them can be incorporated into the inheritance kernel.

Conclusion

Despite the challenges in estimating LD and fitness effects of linked genomic architectures (Box 1), simple approximations can be obtained by treating them as single loci of large effect. This approach was shown to be more powerful for detecting genotype-environment associations between linked haploblocks in *Helianthus* sunflowers compared to characterizing genotypes based on SNPs within the blocks (Todesco *et al.* 2019). When the genomic architecture is not known, a precautionary approach considers the greater variability and higher uncertainty that might be common under a single-locus scenario (also see Kardos & Luikart 2019). Rapid developments in the fields of recombination rate variation and the population genomics of structural variants will continue to improve predictions borne from genomic data.

387

388 Implementing genomic architecture into spatially or temporally explicit conservation and
389 management plans presents additional considerations. For example, variable rates of gene
390 flow within species could result in different genomic architectures underlying adaptation
391 at different spatial and temporal scales (Nosil *et al.* 2009; Oomen 2019). The same trait
392 could be under selection at both scales, as contrasting genomic architectures can produce
393 similar phenotypic outcomes (Therkildsen *et al.* 2019). The diversity of genomic
394 architectures underlying the same or different traits also complicates the process of
395 delineating evolutionarily significant units for conservation, particularly when the relative
396 fitness consequences of trait variation is unclear (Waples & Lindley 2018; Waples *et al.*
397 2019). Nonetheless, it is clear that we must consider linked genomic architectures
398 underlying adaptive traits when predicting the consequences of environmental
399 disturbance to natural populations.

400 **Box 1**

401 **A better understanding of how linked architectures evolve is needed**

402

403 *Linkage disequilibrium should be included in theoretical models*

404

405 A major challenge to modelling the evolution of linked genomic architectures lies in
406 estimating and parameterizing LD, which depends on the distance and epistasis among
407 loci, chromosome size, position of loci along a chromosome, local sequence content, and
408 other sources of recombination rate and gene conversion variation, such as genic
409 modifiers and structural genomic polymorphisms (Figure 2; Kong *et al.* 2002; Butlin
410 2005). Rates of recombination and gene conversion are difficult to estimate directly and
411 vary within and among taxa. Fine-scale crossover maps (Rowan *et al.* 2019) and
412 estimates of recombination (Guerrero & Kirkpatrick 2014) and gene conversion (Korunes
413 & Noor 2019) rates can be obtained with high-throughput sequencing of the offspring of
414 heterozygotes. LD can also be estimated from individual-level population-scale genomic
415 data (Gianola *et al.* 2013; Bilton *et al.* 2018; Ragsdale & Gravel 2019). Yet, even if
416 accurate estimates of LD are obtained for a particular set of environmental conditions,

recombination rates are often plastic (Stevison *et al.* 2017), complicating estimates of LD under environmental change.

Linked architectures have fitness effects besides those of the target phenotype

Besides effects of the trait that is the target of selection, other aspects of linked genomic architectures impact fitness and, consequently, the evolutionary trajectory of the architecture and trait. For example, linked architectures can prevent the purging of deleterious mutations, reducing the fitness of homozygotes (Jay *et al.* 2019). Conversely, heterozygotes for linked architectures can experience partial sterility due to the production of inviable gametes during meiosis, although strong evidence for this appears limited to plants (Hoffmann & Rieseberg 2008). Whether species outside of *Diptera* can displace crossovers away from the breakpoints of chromosomal rearrangements, thus altering their patterns of inheritance, is also poorly understood, as is taxonomic variation in other types of recombination modifiers. Further, there is some probability of developing genetic incompatibilities at linked loci, which could be modelled explicitly. Finally, a better understanding of how eco-evolutionary feedbacks shape genomic architectures is needed.

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800

Table captions

Table 1: Genomic regions in linkage disequilibrium that are associated with environmental or life history traits under selection.

Figure captions

Figure 1: The evolution of age at maturity in Atlantic salmon in response to fishing under hypothetical (a,c) single- and (b,d) multi-locus scenarios for genetic architecture of the trait. The beginning and end of the fishing period with fishing mortality of 0.20 are indicated by dashed vertical lines. Each line represents one replicate simulation (N=10). The top panels show all replicate simulations overlaid on each other, whereas the bottom panels show each replicate on a separate row.

Figure 2: Linkage disequilibrium exists on a spectrum influenced by several factors potentially affecting recombination rate (r) among loci. Rather than a mechanistically accurate diagram, consider this figure as a roughly organized corkboard onto which the various factors and conditions have been pinned.

Figure 3: Hypothetical genomic architectures (top row), corresponding model parameters (middle row), and evolutionary simulations (bottom row) for a polygenic trait in a diploid individual with two chromosomes that is under a temporary period of directional selection (grey bars): (a) a single locus of large effect, (b) ten loci of small effect with negligible linkage disequilibrium (LD), and (c) ten loci of small effect with strong LD. Red bars indicate the position of individual loci along a chromosome. Model parameters include the number of loci (N_{loci}), their effect sizes, and the degree of LD among them (when applicable), whereby continuous dashed lines indicate negligible levels of LD and continuous solid lines indicate strong LD. Individual black lines represent hypothetical replicate simulations (N=3).

Table 1: Genomic regions in linkage disequilibrium that are associated with environmental or life history traits under selection.

Species name	**Common name**	**Variant architecture**	**Variant names and/or locations**	**Associated phenotype**	**References**
Plants					
Boechera stricta	Drummond's rockcress	inversion	LG1	environmental adaptation (water regime)	(Lee *et al*. 2017)
Helianthus spp.	sunflower	haploblocks and inversions	genome-wide (*N*=37)	environmental adaptation (climate) and reproduction (morphology)	(Todesco *et al*. 2019)
Mimulus guttatus	monkeyflower	inversion	DIV1 on chromosome 8	perenniality	(Lowry & Willis 2010; Twyford & Friedman 2015; Coughlan & Willis 2019)
Zea mays ssp. *mays*	highland maize	inversion	Inv4m	environmental adaptation (highland)	(Crow *et al*. 2019)
Invertebrates					
Anopheles spp.	mosquito	inversions	genome-wide (*N*=17)	environmental adaptation (latitudinal clines, altitude-associated habitat)	(Ayala *et al*. 2014, 2017)
Apis mellifera	East African honeybee	inversions	r7, r9	environmental adaptation (altitude-associated habitat)	(Wallberg *et al*. 2017; Christmas *et al*. 2019)
Coelopa frigida	seaweed fly	inversion	chromosome 1	environmental adaptation (latitudinal clines)	(Merot *et al*. 2018; Mérot *et al*. 2019)
Drosophila melanogaster	fruit fly	inversions	In(3R)Payne (3RP), In(3L)P, In(3R)C, In(2L)t	environmental adaptation (latitudinal and altitudinal clines)	(Krimbas & Powell 1992; Anderson *et al*. 2005; Rane *et al*. 2015; Kapun & Fabian 2016; Kapun & Flatt 2019)
Drosophila mojavensis	fruit fly	inversions	chromosome 2 (*N*=7)	environmental adaptation (desert and/or host plant)	(Guillén & Ruiz 2012)
Drosophila pseudoobscura	fruit fly	inversions	AR, PP, CH, ST, TL	environmental adaptation (latitudinal clines)	(Schaeffer 2008; Fuller *et al*. 2016, 2017)
Littorina saxatilis	rough periwinkle	inversions, putative inversions	genome-wide (*N*=17)	environmental adaptation (wave vs. crab ecotype, low-shore vs. high shore)	(Faria *et al*. 2019; Morales *et al*. 2019)
Teleosts					

Species name	Common name	Variant architecture	Variant names and/or locations	Associated phenotype	References
Gadus morhua	Atlantic cod	inversions	LG02, LG07, LG12	environmental adaptation (latitudinal and salinity clines)	(Bradbury *et al*. 2010; Berg *et al*. 2015; Sodeland *et al*. 2016; Barth *et al*. 2017, 2019)
		inversion	LG01	migratory behaviour	(Berg *et al*. 2016, 2017; Kirubakaran *et al*. 2016; Kess *et al*. 2019)
Menidia menidia	Atlantic silverside	block of differentiation	chromosome 24	environmental adaptation (latitudinal clines), growth	(Therkildsen *et al*. 2019)
Salmo salar	Atlantic salmon	fusion	Ssa08/Ssa29	environmental adaptation (summer precipitation)	(Wellband *et al*. 2019)
		linked genomic region	Ssa09	sea age at maturity, run timing	(Johnston *et al*. 2014; Barson *et al*. 2015; Cauwelier *et al*. 2018)
Oncorhynchus mykiss	rainbow trout	double inversion	Omy05	migratory behaviour (anadromous vs. resident and fluvial vs. adfluvial), environmental adaptation (latitudinal and temperature clines)	(Pearse *et al*. 2014, 2019; Arostegui *et al*. 2019)
Oncorhynchus nerka	sockeye salmon	linked genomic region	Ssa09 homolog	environmental adaptation (stream- vs. lake-spawning ecotypes)	(Veale & Russello 2017)
Clupea harengus	Atlantic herring	inversion	chromosome 12	environmental adaptation (latitudinal clines), spawning time	(Barrio *et al*. 2016; Lamichhaney *et al*. 2017; Fuentes-Pardo *et al*. 2019; Pettersson *et al*. 2019)
Oncorhynchus tshawytscha	Chinook salmon	linked genomic region	Ots28	timing of arrival to spawning grounds	(Narum *et al*. 2018)
Ammodytes tobianus	lesser sandeel	haploblock	unknown (13 linked SNPs)	putative environmental adaptation (sea bottom temperature)	(Jiménez-Mena *et al*. 2019)
Oncorhynchus mykiss	steelhead trout	linked genomic region	Omy28	migration timing	(Micheletti *et al*. 2018)
Mallotus villosus	capelin	fusion	chromosome 2 and 9	environmental adaptation (spawning site, temperature)	(Cayuela *et al*. 2019)

Species name	Common name	Variant architecture	Variant names and/or locations	Associated phenotype	References
Gasterosteus aculeatus	three-spined stickleback	inversions	chromosome 1, 11, and 21	environmental adaptation (marine vs. freshwater)	(Jones *et al*. 2012)
Pleuronectes platessa	European plaice	putative inversions	SV19, SV21	environmental adaptation (latitudinal and salinity clines)	(Le Moan *et al*. 2019a; b)
Aves					
Uria aalge	common murre	complex copy number variant	scaffold 72	plumage colouration, thermal adaptation	(Tigano *et al*. 2018)

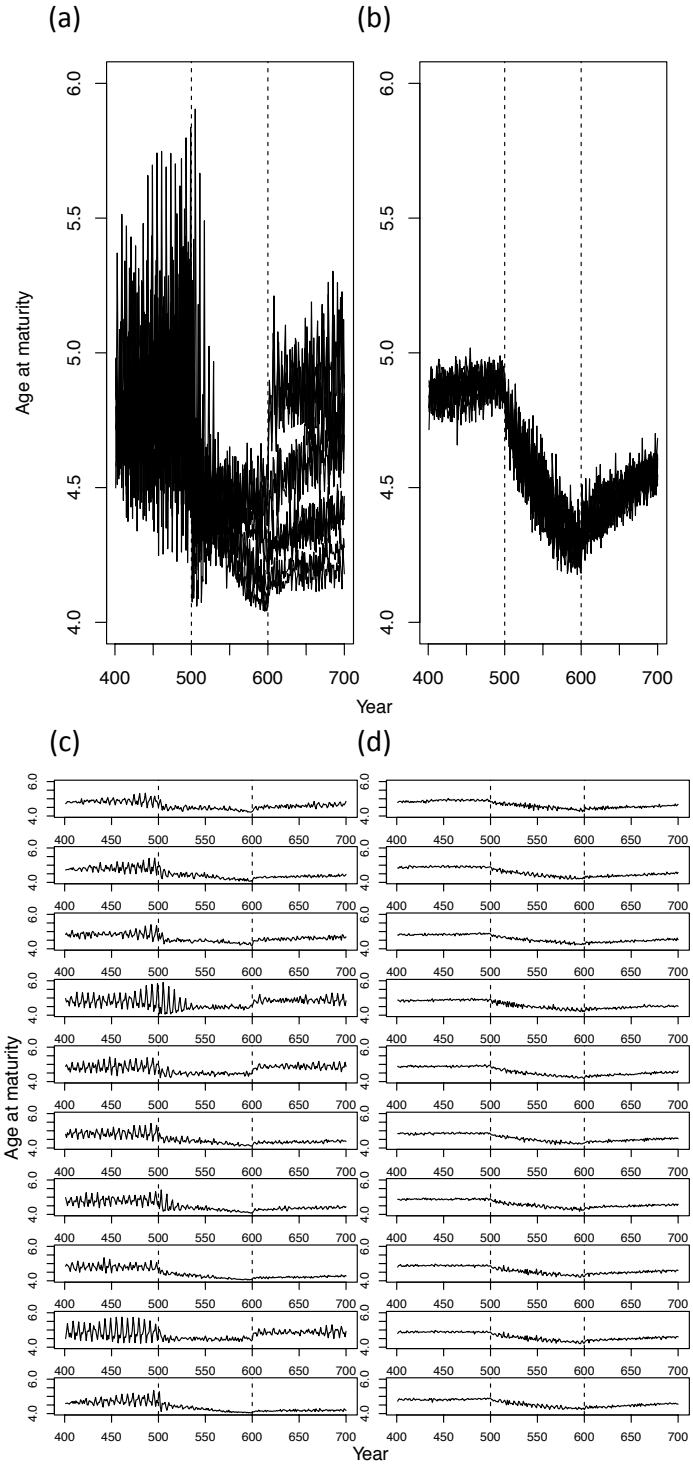

Figure 1: The evolution of age at maturity in Atlantic salmon in response to fishing under hypothetical (a,c) single- and (b,d) multi-locus scenarios for genetic architecture of the trait. The beginning and end of the fishing period with fishing mortality of 0.20 are indicated by dashed vertical lines. Each line represents one replicate simulation (*N*=10). The top panels show all replicate simulations overlaid on each other, whereas the bottom panels show each replicate on a separate row.

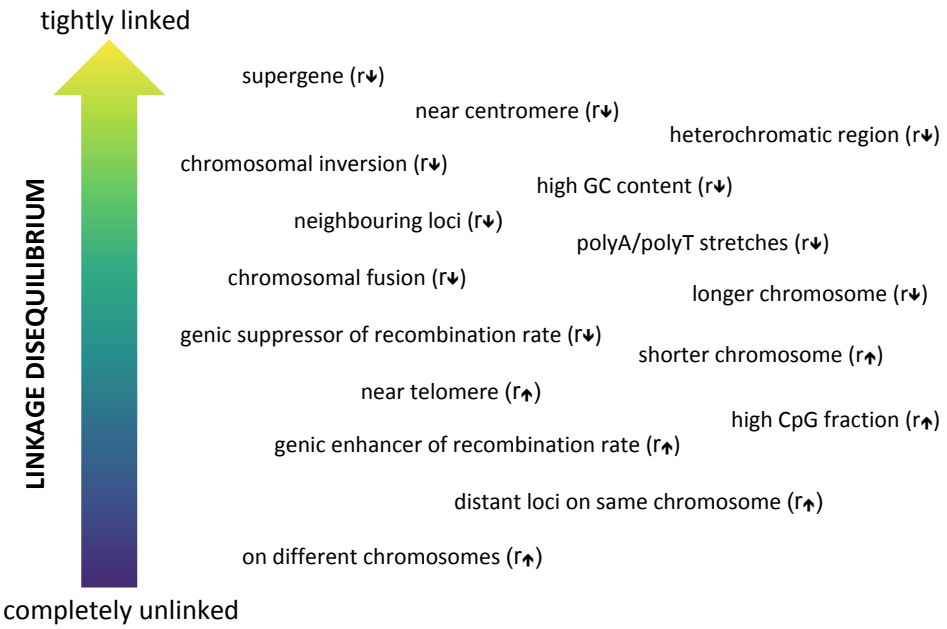

Figure 2: Linkage disequilibrium exists on a spectrum influenced by several factors potentially affecting recombination rate (r) among loci. Rather than a mechanistically accurate diagram, consider this figure as a roughly organized corkboard onto which the various factors and conditions have been pinned.

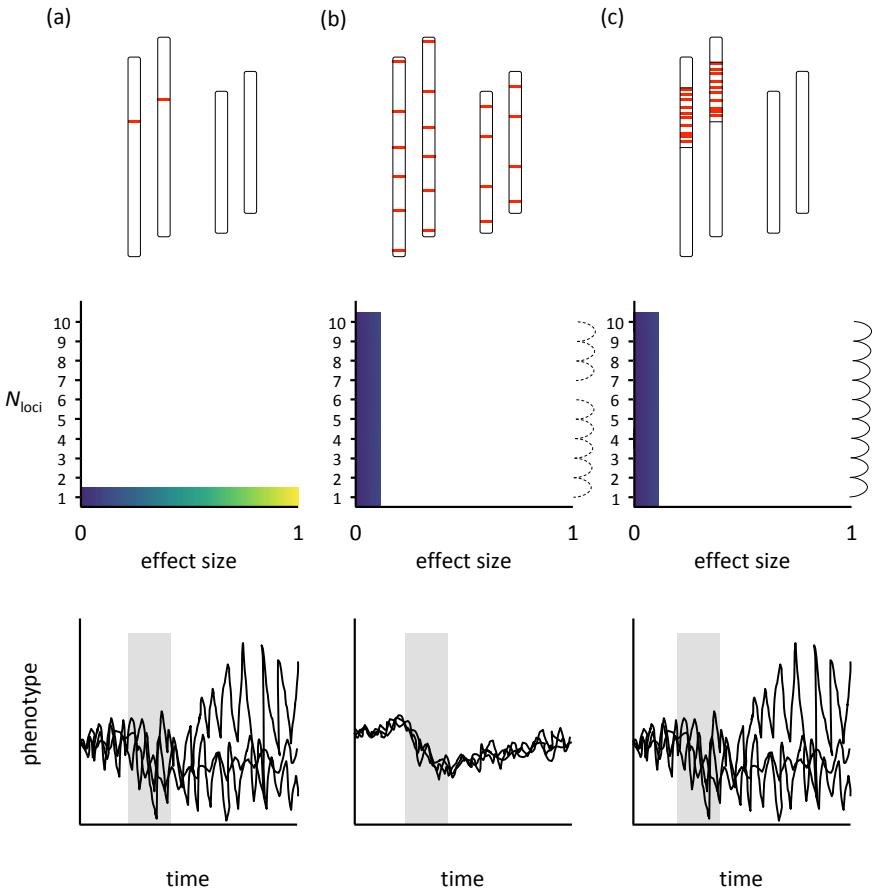

Figure 3: Hypothetical genomic architectures (top row), corresponding model parameters (middle row), and evolutionary simulations (bottom row) for a polygenic trait in a diploid individual with two chromosomes that is under a temporary period of directional selection (grey bars): (a) a single locus of large effect, (b) ten loci of small effect with negligible linkage disequilibrium (LD), and (c) ten loci of small effect with strong LD. Red bars indicate the position of individual loci along a chromosome. Model parameters include the number of loci (N_{loci}), their effect sizes, and the degree of LD among them (when applicable), whereby continuous dashed lines indicate negligible levels of LD and continuous solid lines indicate strong LD. Individual black lines represent hypothetical replicate simulations (N=3).