

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

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23 **Running title:** Genomic architecture shapes evolutionary responses

24 **Abstract**

25

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

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

50 **Eco-evolutionary responses hinge on genetic and genomic architecture**

51

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

61

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

69

70 Here, we discuss some effects of genetic (the number of loci and their effect sizes) and
71 genomic (the degree of linkage among loci) architectures on predictions of evolutionary
72 responses to environmental disturbance. Single or unlinked loci have received
73 comparatively more attention than linked genomic architectures in this regard (Bay *et al.*
74 2017a; Kardos & Luikart 2019). We demonstrate that hypothetical single locus control of
75 a life history trait under harvesting-induced selection generates a more variable
76 evolutionary response compared to an unlinked polygenic scenario. We then suggest that
77 linked polygenic architectures resemble those of single large-effect loci, yet exist along a
78 continuum of linkage disequilibrium, and are likely to play a large role in adaptation to
79 rapid environmental change. We show that linked architectures underlie diverse traits in
80 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 *vgl3* 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

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

115

116 *Single-locus architecture generates divergent evolutionary responses to harvesting*

117

118 We revisited this model to compare hypothetical single- and multi-locus architectures,
119 but without dimorphic trait expression, to assess whether genetic architecture affected
120 trait evolution in a more general scenario absent of sexual dimorphism. To this end, we
121 took simple averages of the sex-specific probabilities for the male and female age at
122 maturity. By doing this, a male and a female carrying the same single-locus genotype
123 have the same probabilities to mature at the ages of 1SW, 2SW and 3 SW. We simulated
124 10 independent evolutionary trajectories for both the single-locus and the multi-locus
125 control scenarios and tracked the average age at maturity for each simulation time step.
126 The simulations involved three phases: i) pristine conditions in the absence of fishing
127 (500 years, the first 400 of which were discarded as burn-in), ii) exposure to selective
128 fishing mortality at the rate of 0.2, and iii) recovery in the absence of fishing. The
129 detailed model description and parameter values are reported in Kuparinen & Hutchings
130 (2017).

131

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

266

267 Linked architectures associated with adaptation to local environmental variables seem
268 particularly common among flies and fishes (Table 1; Wellenreuther & Bernatchez
269 2018). Flies in the genus *Drosophila* provide numerous examples of inversions associated
270 with environmental adaptation, including those exhibiting latitudinal (Krimbas & Powell
271 1992; Anderson *et al.* 2005; Rane *et al.* 2015; Fuller *et al.* 2016, 2017; Kapun & Fabian
272 2016; Kapun & Flatt 2019) and altitudinal (Kapun & Flatt 2019) clines, as well as
273 adaptation to a desert environment (possibly through the host plant; Guillén & Ruiz
274 2012). Of particular interest from a human health perspective, environmentally structured
275 inversion polymorphisms are common among *Anopheles* spp. mosquitos, potentially
276 enhancing the adaptability and vector potency of these primary malaria vectors (Ayala *et*
277 *al.* 2014, 2017). Inversions in *Anopheles* spp. vary in karyotype frequencies across
278 latitudinal clines and between mountain forests and lowland savannahs (Ayala *et al.*
279 2017), and are associated with aridity tolerance.

280

281 Inversions and blocks of differentiation (which may or may not be associated with
282 inversions) appear to underlie adaptation to salinity (Jones *et al.* 2012; Berg *et al.* 2015)
283 and vary in frequency across latitudinal clines in marine fishes, suggesting an association
284 with temperature or growing season length (Pettersson *et al.* 2019; Therkildsen *et al.*
285 2019; Kess *et al.* 2020). Chromosomal translocations and fusions are common among
286 salmonids (Phillips 2005). Their adaptive significance, if any, is not generally known,
287 although a fusion in Atlantic salmon (Ssa08/Ssa29) is associated with summer
288 precipitation in a Canadian river system (Wellband *et al.* 2019).

289

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

327 environmental and life history traits. An inversion in Atlantic herring (*Clupea harengus*)
328 is associated with both temperature and timing of reproduction (Fuentes-Pardo *et al.*
329 2019; Pettersson *et al.* 2019), whereas linked regions in Chinook salmon (*O. tshawytscha*;
330 Narum *et al.* 2018) and steelhead (Micheletti *et al.* 2018) are associated with the timing
331 of arrival to spawning grounds.

332

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

345

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

355

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

359

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

361

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

374

375 **Conclusion**

376

377 Despite the challenges in estimating LD and fitness effects of linked genomic
378 architectures (Box 1), simple approximations can be obtained by treating them as single
379 loci of large effect. This approach was shown to be more powerful for detecting
380 genotype-environment associations between linked haploblocks in *Helianthus* sunflowers
381 compared to characterizing genotypes based on SNPs within the blocks (Todesco *et al.*
382 2019). When the genomic architecture is not known, a precautionary approach considers
383 the greater variability and higher uncertainty that might be common under a single-locus
384 scenario (also see Kardos & Luikart 2019). Rapid developments in the fields of
385 recombination rate variation and the population genomics of structural variants will
386 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,

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

419

420 *Linked architectures have fitness effects besides those of the target phenotype*

421

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

435

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- 800

801 **Table captions**

802

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

805

806 **Figure captions**

807

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

814

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

819

820 Figure 3: Hypothetical genomic architectures (top row), corresponding model parameters
821 (middle row), and evolutionary simulations (bottom row) for a polygenic trait in a diploid
822 individual with two chromosomes that is under a temporary period of directional
823 selection (grey bars): (a) a single locus of large effect, (b) ten loci of small effect with
824 negligible linkage disequilibrium (LD), and (c) ten loci of small effect with strong LD.
825 Red bars indicate the position of individual loci along a chromosome. Model parameters
826 include the number of loci (N_{loci}), their effect sizes, and the degree of LD among them
827 (when applicable), whereby continuous dashed lines indicate negligible levels of LD and
828 continuous solid lines indicate strong LD. Individual black lines represent hypothetical
829 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					
<i>Boechera stricta</i>	Drummond's rockcress	inversion	LG1	environmental adaptation (water regime)	(Lee <i>et al.</i> 2017)
<i>Helianthus</i> spp.	sunflower	haploblocks and inversions	genome-wide ($N=37$)	environmental adaptation (climate) and reproduction (morphology)	(Todesco <i>et al.</i> 2019)
<i>Mimulus guttatus</i>	monkeyflower	inversion	DIV1 on chromosome 8	perenniality	(Lowry & Willis 2010; Twyford & Friedman 2015; Coughlan & Willis 2019)
<i>Zea mays</i> ssp. <i>mays</i>	highland maize	inversion	Inv4m	environmental adaptation (highland)	(Crow <i>et al.</i> 2019)
Invertebrates					
<i>Anopheles</i> spp.	mosquito	inversions	genome-wide ($N=17$)	environmental adaptation (latitudinal clines, altitude-associated habitat)	(Ayala <i>et al.</i> 2014, 2017)
<i>Apis mellifera</i>	East African honeybee	inversions	r7, r9	environmental adaptation (altitude-associated habitat)	(Wallberg <i>et al.</i> 2017; Christmas <i>et al.</i> 2019)
<i>Coelopa frigida</i>	seaweed fly	inversion	chromosome 1	environmental adaptation (latitudinal clines)	(Merot <i>et al.</i> 2018; Mérot <i>et al.</i> 2019)
<i>Drosophila melanogaster</i>	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 <i>et al.</i> 2005; Rane <i>et al.</i> 2015; Kapun & Fabian 2016; Kapun & Flatt 2019)
<i>Drosophila mojavensis</i>	fruit fly	inversions	chromosome 2 ($N=7$)	environmental adaptation (desert and/or host plant)	(Guillén & Ruiz 2012)
<i>Drosophila pseudoobscura</i>	fruit fly	inversions	AR, PP, CH, ST, TL	environmental adaptation (latitudinal clines)	(Schaeffer 2008; Fuller <i>et al.</i> 2016, 2017)
<i>Littorina saxatilis</i>	rough periwinkle	inversions, putative inversions	genome-wide ($N=17$)	environmental adaptation (wave vs. crab ecotype, low-shore vs. high shore)	(Faria <i>et al.</i> 2019; Morales <i>et al.</i> 2019)
Teleosts					

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

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

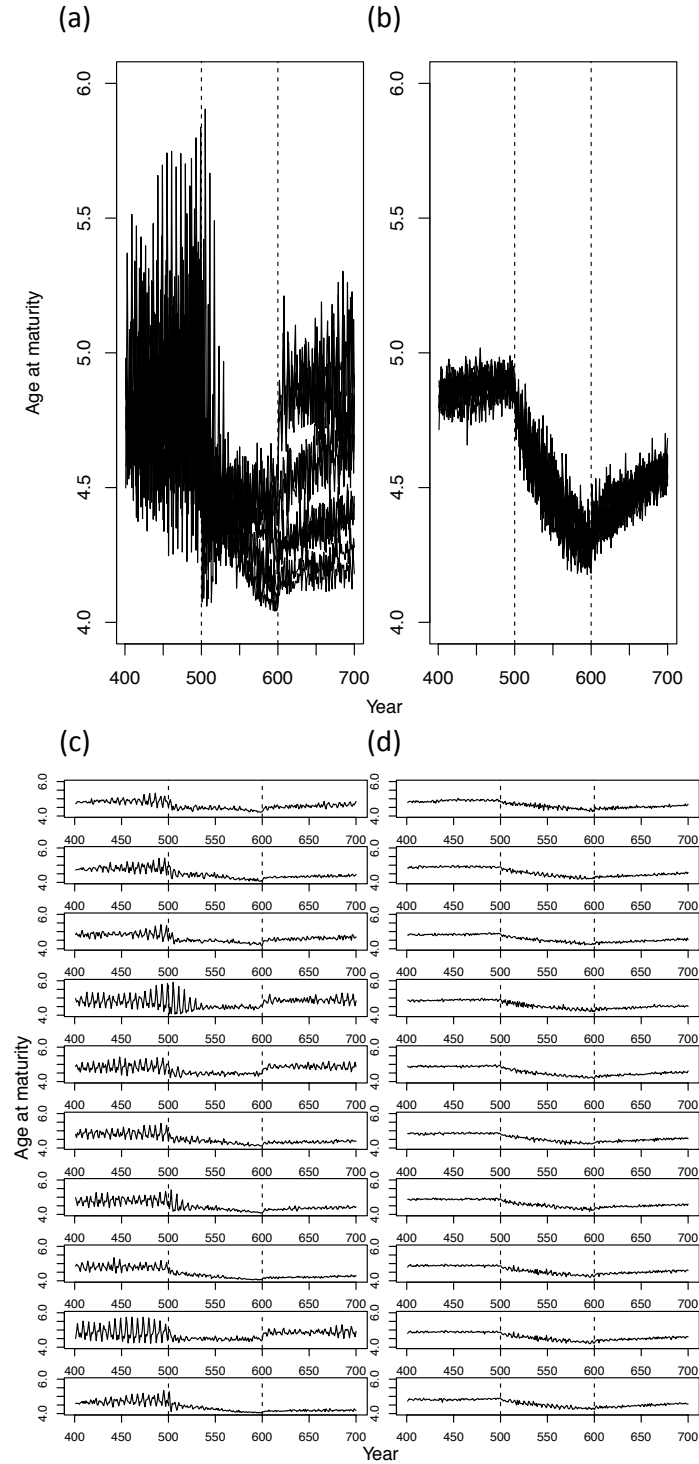


Figure 1: The evolution of age at maturity in Atlantic salmon in response to fishing under hypothetical (a,c) single- and (b,d) multi-locus scenarios for genetic architecture of the trait. The beginning and end of the fishing period with fishing mortality of 0.20 are indicated by dashed vertical lines. 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.

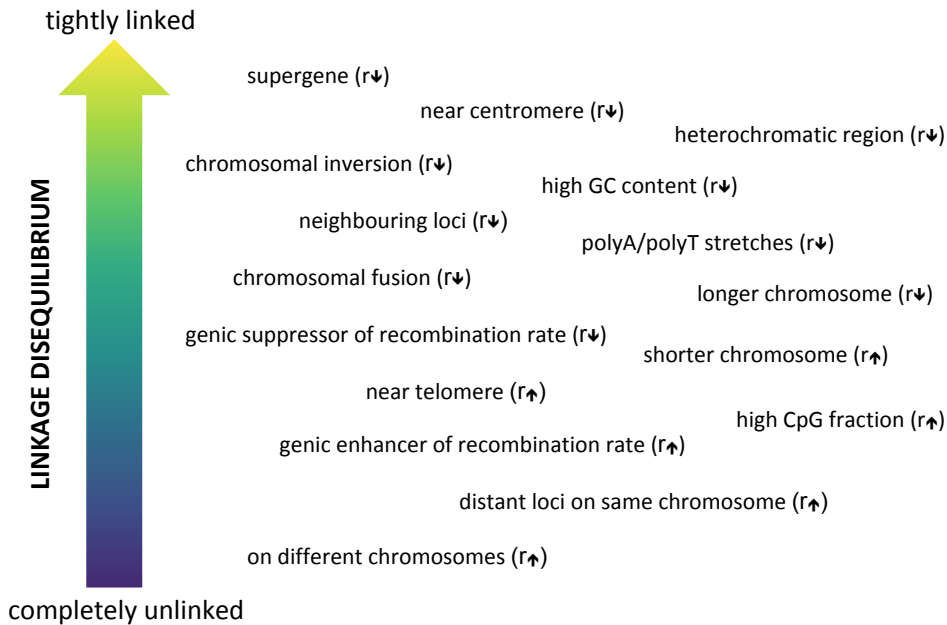


Figure 2: Linkage disequilibrium exists on a spectrum influenced by several factors potentially affecting recombination rate (r) among loci. Rather than a mechanistically accurate diagram, consider this figure as a roughly organized corkboard onto which the various factors and conditions have been pinned.

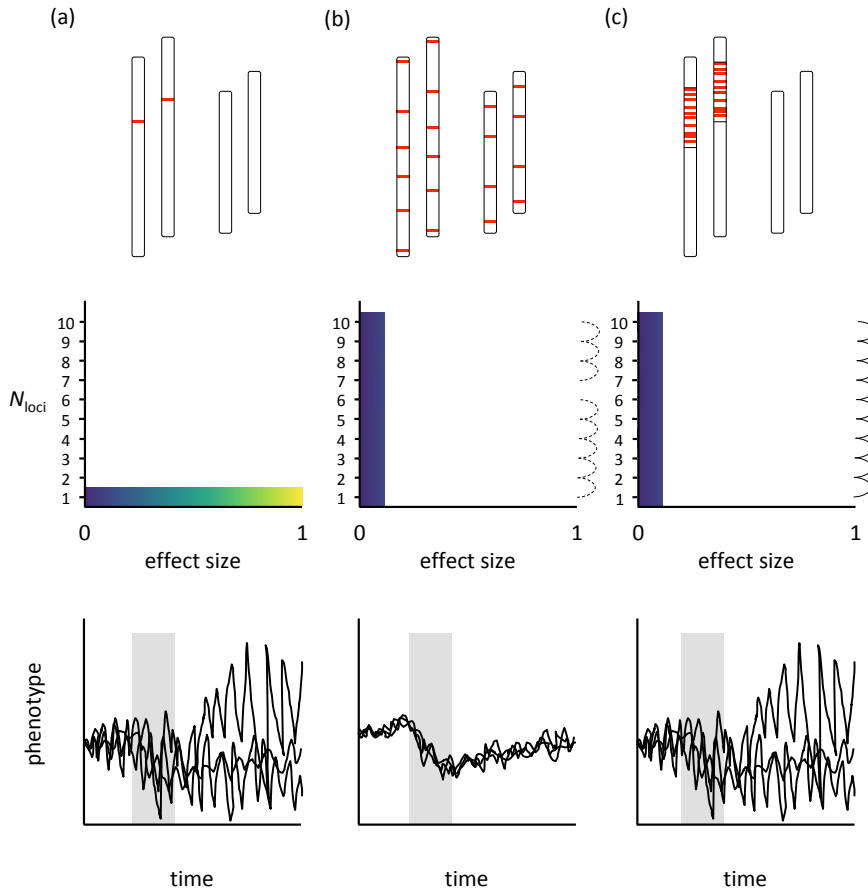


Figure 3: Hypothetical genomic architectures (top row), corresponding model parameters (middle row), and evolutionary simulations (bottom row) for a polygenic trait in a diploid individual with two chromosomes that is under a temporary period of directional selection (grey bars): (a) a single locus of 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 ($N=3$).