

NEWS AND VIEWS**Perspective**

Linked selection, demography and the evolution of correlated genomic landscapes in birds and beyond

Reto Burri 

Department of Population Ecology,
Friedrich Schiller University Jena, Jena,
Germany

Correspondence

Reto Burri, Department of Population
Ecology, Friedrich Schiller University Jena,
Jena, Germany.
Email: burri@wildlight.ch

Abstract

Selection has a deep impact on the distribution of genetic diversity and population differentiation along the genome (the genomic landscapes of diversity and differentiation), reducing diversity and elevating differentiation not only at the sites it targets, but also at linked neutral sites. Fuelled by the high-throughput sequencing revolution, these genomic footprints of selection have been extensively exploited over the past decade with the aim to identify genomic regions involved in adaptation and speciation. However, while this research has shown that the genomic landscapes of diversity and differentiation are usually highly heterogeneous, it has also led to the increasing realization that this heterogeneity may evolve under processes other than adaptation or speciation. In particular, instead of being an effect of selective sweeps or barriers to gene flow, accentuated differentiation can evolve by any process reducing genetic diversity locally within the genome (Charlesworth, 1998), including purifying selection at linked sites (background selection). In particular, in genomic regions where recombination is infrequent, accentuated differentiation can evolve as a by-product of diversity reductions unrelated to adaptation or speciation (Cruickshank & Hahn, 2014; Nachman & Payseur, 2012; Noor & Bennett, 2009). In such genomic regions, linkage extends over physically larger genome stretches, and selection affects a particularly high number of linked neutral sites. Even though the effects of selection on linked neutral diversity (linked selection) within populations are well documented (Cutter & Payseur, 2013), recent observations of diversity and differentiation landscapes that are highly correlated even among independent lineages suggest that the effects of long-term linked selection may have a deeper impact on the evolution of the genomic landscapes of diversity and differentiation than previously anticipated. The study on *Saxicola* stonechats by Van Doren et al. (2017) reported in the current issue of *Molecular Ecology* lines in with a rapidly expanding body of evidence in this direction. Correlations of genomic landscapes extending from within stonechats to comparisons with *Ficedula* flycatchers add to recent insights into the timescales across which the effects of linked selection persist. Absent and inverted correlations of genomic landscapes in comparisons involving an island taxon, on the other hand, provide important empirical clues about the role of demographic constraints in the evolution of the genomic landscapes of diversity and differentiation.

KEYWORDS

adaptation, effective population size, genome scans, recombination rate variation, speciation

The genomic landscape of differentiation is usually highly heterogeneous, with regions of accentuated differentiation widespread across the genome. Although this is one of the best consolidated patterns established by a decade's efforts to identify genomic regions involved in adaptation and speciation (e.g., Burri et al., 2015; Irwin, Alcaide, Delmore, Irwin, & Owens, 2016; Martin et al., 2013; Renaut, Owens, & Rieseberg, 2014; Vijay et al., 2016), the processes involved in its evolution remain more controversial. Originally interpreted as a footprint of selective sweeps or selection against gene flow, accentuated differentiation has now repeatedly been associated with genomic regions of low recombination (e.g., Burri et al., 2015), suggesting an important role for linked selection in its evolution. Awareness is therefore rising that not only positive selection associated with adaptation or speciation, but also background selection, can have an important role in driving the evolution of the genomic landscapes of diversity and differentiation.

However, as suggested by previous studies in various organisms (Burri et al., 2015; Irwin et al., 2016; Martin et al., 2013; Phung, Huber, & Lohmueller, 2016; Renaut et al., 2014), and now consolidated by Van Doren et al. (2017), linked selection may have further reaching consequences than anticipated so far, putting even the previous golden standard practice of replication and the inference of parallel evolution into the line of fire. The replication of accentuated differentiation in the same genomic region in independent experiments (e.g., multiple altitudinal gradients, multiple hybrid zones) is perceived as confirmatory for such a region's involvement in adaptation (or speciation). However, the correlations of genomic landscapes among closely related species reported by Van Doren et al. (2017) in stonechats (Figure 1, centre) and previously documented in flycatchers (Figure 1, right; Burri et al., 2015), crows (Figure 1, left; Vijay et al., 2016), greenish warblers (Irwin et al., 2016), *Heliconius* butterflies (Martin et al., 2013) and *Helianthus* sunflowers (Renaut et al., 2014) document highly replicated accentuated differentiation among

closely related species as a widespread phenomenon. What is more, the study by Van Doren et al. (2017) does not make halt at the genus level. Together with two other recent studies (Dutoit et al., 2017; Vijay et al., 2017) it goes further to document that correlated genomic landscapes in birds have persisted over tens of millions of years, making a strong case for genomic features—in particular recombination rate—in governing the genomic landscapes of diversity and differentiation. Indeed, the observed correlations are a direct prediction of long-term linked selection in heterogeneous recombination landscapes that are conserved among species (Burri, 2017). In genome regions in which low-recombination rate is conserved across multiple consecutive speciation events, the diversity-reducing effects of linked selection accumulate across extended periods of time. As a result, along with heterogeneous recombination landscapes, ancestors transmit a diversity landscape to their daughter species whose heterogeneity may continue to be maintained by linked selection for as long as the recombination landscape persists (Burri, 2017). The extended periods of time across which this process is active have two notable implications: the slow process of background selection alone might suffice for the evolution of correlated differentiation landscapes (Phung et al., 2016), and sweeps in the ancestral (as opposed to extant) lineage may make contributions to extant genomic landscapes of diversity and differentiation (Munch, Nam, Schierup, & Mailund, 2016). In species with long-term conserved broad-scale recombination landscapes, such as birds, the replication of accentuated differentiation may therefore not be informative regarding a genomic region's involvement in adaptation or speciation, nor indicative of parallel ecology-related evolution.

To further complicate the issue, demographic effects can act to enhance or counter the effects of linked selection (Burri, 2017). Even with the underlying recombination landscape conserved, whether or not correlated genomic landscapes evolve—and whether the problems with replication and with the inference of parallel evolution



FIGURE 1 Avian systems exhibiting correlated differentiation landscapes. Left: *Corvus* crows; hooded crow (*Corvus cornix*), Uppsala, Sweden (top); carrion crow (*Corvus corone*), Chablais de Cudrefin, Switzerland (bottom). Centre: Siberian stonechat (*Saxicola maurus*), Sat Tal, Kumaon hills, India. Right: *Ficedula* flycatchers; collared flycatcher (*Ficedula albicollis*), Öland, Sweden (top); pied flycatcher (*Ficedula hypoleuca*), Uppsala, Sweden (bottom). Photographs: Reto Burri

outlined above apply—may depend on the efficiency of (linked) selection, and thus genomewide effective population size (N_e). Linked selection appears to reduce genetic diversity across a smaller range of low-recombination rates in species with low N_e (Corbett-Detig, Hartl, & Sackton, 2015), for instance. In strongly bottlenecked species, the effects of linked selection may be even further reduced. In such species, the diversity landscape is expected to correlate less with those of related species, and the according differentiation landscapes distorted. Van Doren et al. (2017) present results from an island endemic, the Canary Islands stonechats (*S. dacotiae*), that fit this hypothesis. Unsurprisingly, baseline diversity (although not average diversity) appears lowest in this species (Van Doren et al., 2017, fig. S8). Perhaps more surprisingly, the heterogeneity of diversity across the genome of this species is significantly reduced compared to congeners (variance of π across autosomes: $0.50 \cdot 10^{-6}$, compared to $1.1\text{--}3.6 \cdot 10^{-6}$), resulting in an average genetic diversity similar to most congeners (mean autosomal π : $2.3 \cdot 10^{-3}$, versus $2.3\text{--}2.8 \cdot 10^{-3}$ in *Saxicola torquatus* and *Saxicola rubicola* ssp., $4.8 \cdot 10^{-3}$ in *Saxicola maurus*). Most remarkably, genetic diversity in this island endemic nowhere in the genome reaches the low values observed in many regions of the other *Saxicola* species (minimum π : *Saxicola dacotiae*, $1.3 \cdot 10^{-3}$; compared to $0.2\text{--}0.5 \cdot 10^{-3}$). The observation that in these genome regions, Canary Islands stonechats exhibit higher extant diversity than expected from ancestral diversity (i.e., π/d_{XY} is high; Van Doren et al., 2017, fig. S8) is in line with linked selection being less efficient in this species than in its ancestor.

The reduced efficiency of selection in Canary Islands stonechats not only leads to reduced correlations of the diversity landscapes in comparisons including this species. It also strongly impacts the differentiation landscape (F_{ST}) and its relationship with divergence (d_{XY}), in particular when involving comparisons between Canary Islands and African stonechats (*S. torquatus*). Between these species, several regions display reduced differentiation but show elevated differentiation in comparisons among congeners (Van Doren et al., 2017, fig. S5). Moreover, the correlation of differentiation with divergence between these species is inverted compared to other species comparisons (Van Doren et al., 2017, figure 3B–C). Both observations fit a scenario in which genetic drift dominates over the effects of linked selection. For accentuated differentiation ($F_{ST} = (\pi_{\text{total}} - \pi_{\text{within}})/\pi_{\text{total}}$) to evolve in low-recombination regions after a lineage split, either linked selection or drift needs to continue acting at higher rates than in the surroundings, such that the reduction in within-population diversity (π_{within}) exceeds the according reduction in total diversity ($\pi_{\text{total}} \sim d_{XY}$). In Canary Islands stonechats, however, this is not the case. Rather, as indicated by elevated π/d_{XY} ratios (Van Doren et al., 2017, fig. S9), the processes that have reduced diversity in these regions in the ancestor have halted, and genetic variation replenished (note that π/d_{XY} is closely related to F_{ST} , as the latter can be rewritten as $F_{ST} = 1 - \pi_{\text{within}}/\pi_{\text{total}}$, and $\pi_{\text{total}} \sim d_{XY}$). Due to a rather homogeneous differentiation landscape in Canary Islands stonechats, total diversity appears to dominate in determining differentiation patterns, resulting in high differentiation in regions of high divergence, and low differentiation in regions of low divergence. This

behaviour of the differentiation landscape also explains the shift from a negative (as expected under linked selection) to the observed positive correlation of differentiation with divergence. These results illustrate how demographic events, such as a presumed founder effect, can distort the correlations among genomic landscapes that would else be expected under a model of linked selection.

In summary, the results reported by Van Doren et al. (2017) consolidate a model in which linked selection in a conserved recombination landscape can replicate highly congruent genomic landscapes of diversity and differentiation over tens of millions of years (Burri, 2017). The extent to which in Canary Islands stonechats genetic diversity was replenished in genomic regions in which it is otherwise strongly reduced (in congeners and in the ancestor) further highlights the magnitude of constraints imposed by linked selection. Empirical research will have to show over which timescales similar constraints may lead to long-term correlated genomic landscapes in organisms other than birds. A detailed characterization of recombination rates is required to gain direct evidence for the role of recombination rate evolution in the evolution of correlated diversity and differentiation landscapes. Finally, the case of the Canary Islands stonechat illustrates how demographic effects can shift single species entirely away from genomic landscapes otherwise strongly correlated among congeners. Consequently, caveats with the interpretation of genomic landscapes may be individual to each taxon, and a comparative perspective as taken and advocated by Van Doren et al. (2017) and others (e.g., Burri, 2017) may be required to assess the specific constraints that linked selection, demography and other processes impose upon the genomic landscapes under investigation.

AUTHOR CONTRIBUTIONS

R.B. conceived and wrote the article.

REFERENCES

- Burri, R. (2017). Interpreting differentiation landscapes in the light of long-term linked selection. *Evolution Letters*, (accepted).
- Burri, R., Nater, A., Kawakami, T., Mugal, C. F., Olason, P. I., Smeds, L., ... Ellegren, H. (2015). Linked selection and recombination rate variation drive the evolution of the genomic landscape of differentiation across the speciation continuum of *Ficedula* flycatchers. *Genome Research*, 25, 1656–1665.
- Charlesworth, B. (1998). Measures of divergence between populations and the effect of forces that reduce variability. *Molecular Biology and Evolution*, 15, 538–543.
- Corbett-Detig, R. B., Hartl, D. L., & Sackton, T. B. (2015). Natural selection constrains neutral diversity across a wide range of species. *PLoS Biology*, 13, e1002112.
- Cruickshank, T. E., & Hahn, M. W. (2014). Reanalysis suggests that genomic islands of speciation are due to reduced diversity, not reduced gene flow. *Molecular Ecology*, 23, 3133–3157.
- Cutter, A. D., & Payseur, B. A. (2013). Genomic signatures of selection at linked sites: Unifying the disparity among species. *Nature Reviews Genetics*, 14, 262–274.
- Dutoit, L., Vijay, N., Mugal, C. F., Bossu, C. M., Burri, R., Wolf, J. W. B., & Ellegren, H. (2017). Covariation in levels of nucleotide diversity in homologous regions of the avian genome long after completion of

- lineage sorting. *Proceedings of the Royal Society B: Biological Sciences*, 284, 20162756.
- Irwin, D. E., Alcaide, M., Delmore, K. E., Irwin, J. H., & Owens, G. L. (2016). Recurrent selection explains parallel evolution of genomic regions of high relative but low absolute differentiation in a ring species. *Molecular Ecology*, 25, 4488–4507.
- Martin, S. H., Dasmahapatra, K. K., Nadeau, N. J., Salazar, C., Walters, J. R., Simpson, F., ... Jiggins, C. D. (2013). Genome-wide evidence for speciation with gene flow in *Heliconius* butterflies. *Genome Research*, 23, 1817–1828.
- Munch, K., Nam, K., Schierup, M. H., & Mailund, T. (2016). Selective sweeps across twenty millions years of primate evolution. *Molecular Biology and Evolution*, 33, 3065–3074.
- Nachman, M. W., & Payseur, B. A. (2012). Recombination rate variation and speciation: Theoretical predictions and empirical results from rabbits and mice. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 367, 409–421.
- Noor, M. A. F., & Bennett, S. M. (2009). Islands of speciation or mirages in the desert[quest] Examining the role of restricted recombination in maintaining species. *Heredity*, 103, 439–444.
- Phung, T. N., Huber, C. D., & Lohmueller, K. E. (2016). Determining the effect of natural selection on linked neutral divergence across species. *PLoS Genetics*, 12, e1006199.
- Renaut, S., Owens, G. L., & Rieseberg, L. H. (2014). Shared selective pressure and local genomic landscape lead to repeatable patterns of genomic divergence in sunflowers. *Molecular Ecology*, 23, 311–324.
- Van Doren, B. M., Campagna, L., Helm, B., Illera, J. C., Lovette, I. J., & Liedvogel, M. (2017). Correlated patterns of genetic diversity and differentiation across an avian family. *Molecular Ecology*, 26, (3982–3997).
- Vijay, N., Bossu, C. M., Poelstra, J. W., Weissensteiner, M. H., Suh, A., Kryukov, A. P., & Wolf, J. B. W. (2016). Evolution of heterogeneous genome differentiation across multiple contact zones in a crow species complex. *Nature Communications*, 7, 13195.
- Vijay, N., Weissensteiner, M. H., Burri, R., Kawakami, T., Ellegren, H., & Wolf, J. B. W. (2017). Genome-wide signatures of genetic variation within and between populations – a comparative perspective. *Molecular Ecology*, (accepted).

How to cite this article: Burri R. Linked selection, demography and the evolution of correlated genomic landscapes in birds and beyond. *Mol Ecol.* 2017;26:3853–3856. <https://doi.org/10.1111/mec.14167>