

Landscape community genomics: understanding eco-evolutionary processes in complex environments

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Extrinsic factors influencing evolutionary processes are often categorically lumped into interactions that are environmentally (e.g., climate, landscape) or community-driven, with little consideration of the overlap or influence of one on the other. However, genomic variation is strongly influenced by complex and dynamic interactions between environmental and community effects. Failure to consider both effects on evolutionary dynamics simultaneously can lead to incomplete, spurious, or erroneous conclusions about the mechanisms driving genomic variation. We highlight the need for a landscape community genomics (LCG) framework to help to motivate and challenge scientists in diverse fields to consider a more holistic, interdisciplinary perspective on the genomic evolution of multi-species communities in complex environments.

The evolutionary play in the genomic age

The analogy of the ‘ecological theater and the evolutionary play’ has been present in the scientific literature for at least the past five decades [1]. In recent years there has been renewed emphasis on the importance of resolving the interplay between the ‘actors’ and the ‘stage’ that create the evolutionary play (i.e., interacting species and the abiotic environment in which those interactions take place) [2,3]. Explicit consideration of the simultaneous, interactive effects of both biotic and abiotic impacts on evolutionary processes, however, has not been fully incorporated into contemporary approaches aimed at elucidating patterns of genomic variation in populations, species, and ultimately communities. Specifically, the burgeoning field of landscape genetics (see [Glossary](#)) interprets patterns of genetic divergence and diversity based primarily on abiotic or physical variation, whereas community genetics interprets those patterns based on interactions among species

[4,5]. This relatively-narrow focus on either abiotic or biotic drivers of genomic variation is understandable given the past limitations of genetic tools. Fortunately, recent advances in genomic techniques make it feasible to consider the simultaneous influence of the abiotic ‘stage’ and biotic ‘actors’ on the ‘evolutionary play’.

Glossary

Admixture: the formation of novel genetic combinations through hybridization of genetically distinct groups.

Community: an assemblage of at least two interacting species that live in the same geographic area.

Community ecology: the study of the interactions between species in communities on many spatial and temporal scales, including the distribution, structure, abundance, demography, and interactions between coexisting populations.

Community genetics: the study of the genetic consequences of species interactions in a local community, including how a single foundational (or keystone) species shapes specific genotypic and phenotypic characteristics of other members of the community.

Dispersal: permanent movement away from an origin (birthplace) and settlement at a new location.

Eco-evolutionary dynamics: the interaction and feedback between ecological and evolutionary processes.

Exon capture: a technique for sequencing all (or a subset) of the protein-coding genes in a genome (known as the exome). It consists of first isolating only the subset of DNA that encodes proteins (known as exons), and then sequencing that DNA using high-throughput DNA sequencing technology.

Genomics: the study of the structure, function, or variation in a large number of genes or markers throughout a genome.

Hybridization: interbreeding between individuals from genetically distinct populations.

Introgression: the incorporation of genes from one population into another through hybridization that results in fertile offspring that further hybridize and backcross to parental populations.

Landscape community genomics (LCG): the application of genomics to study how neutral and adaptive genomic variation within and among populations of multiple interacting species within communities is shaped by the interaction of abiotic and biotic factors across diverse landscapes.

Landscape genetics: the study of the influence of landscape or climate features on neutral genetic variation within and among populations.

Landscape genomics: the study of the influence of landscape or climate features on neutral and adaptive genetic variation (genome-wide) within and among populations.

Metacommunity: a group of spatially discrete communities of multiple species linked by dispersal.

Metagenomics: the analysis of DNA from the many species contained in an environmental sample, facilitated by high-throughput sequencing.

Massively-parallel sequencing: new DNA sequencing technologies that produce millions of short reads (25–500 nt) in a short time (1–5 days) with reduced cost.

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The genomics age offers tremendous advances in the availability of multi-species genome-wide data and related bioinformatics methods [6,7]. Until now, a comprehensive analytical framework for resolving the drivers of genome evolution has been lacking. With such a framework, genomics promises to increase our understanding of previously intractable questions in evolutionary ecology, population genetics, and conservation biology, including: (i) how do abiotic and biotic factors interactively (and independently) influence patterns of gene flow, drift, and selection in multiple interacting species; (ii) how consistent or general are patterns of co-adaptation among species in geographically isolated communities that reside in different environmental conditions; and (iii) how will environmental change impact upon community composition and subsequent genomic co-evolution?

More broadly, genomics offers unprecedented resolution and statistical power to elucidate evolutionary patterns, including genotype-by-environment interactions [8], effects of local co-adaptation on gene flow [9,10], hybridization [11,12], and in delineation of conservation units based on multiple interacting species [13,14]. Nevertheless, realizing this potential will require a fundamental conceptual and analytical shift in assessment of genomic variation. Our goal here is to show the need for this conceptual shift by introducing a novel LCG framework that merges a diverse set of sub-disciplines in evolutionary biology and ecology.

Why LCG?

The study of evolution and adaptation in nature should consider how abiotic and biotic drivers influence various evolutionary processes and resulting patterns of genomic variation. Unfortunately, analyses and interpretation of patterns of genomic variation are often biased by the particular discipline with which researchers identify themselves (e.g., as a landscape geneticist, community geneticist, or landscape epidemiologist).

Landscape genetics generally lacks consideration of how localized interactions among species affect genomic evolution (e.g., competition, predation, co-adaptation, etc.), and instead focuses on the spatial arrangement of populations and the structure of the intervening habitat [15]. Fundamental evolutionary processes such as dispersal are often viewed as stochastic and independent of local ecological interactions, partly because the effects of co-adaptation on dispersal are poorly understood [16]. In cases where mechanistic understanding is limited, simply examining patterns of genetic variation in interacting species can highlight important differences in the drivers of genetic structure (Figure 1). For example, in a symbiotic beetle–fungal system, beetle genetic variation was dependent on environment and host density (pine tree volume) whereas fungus genetic variation was not [17]. In a different host–parasite system, the genetic structure of the parasite better predicted host population structure than did host genotypes [14]. Despite the value of testing for concordant

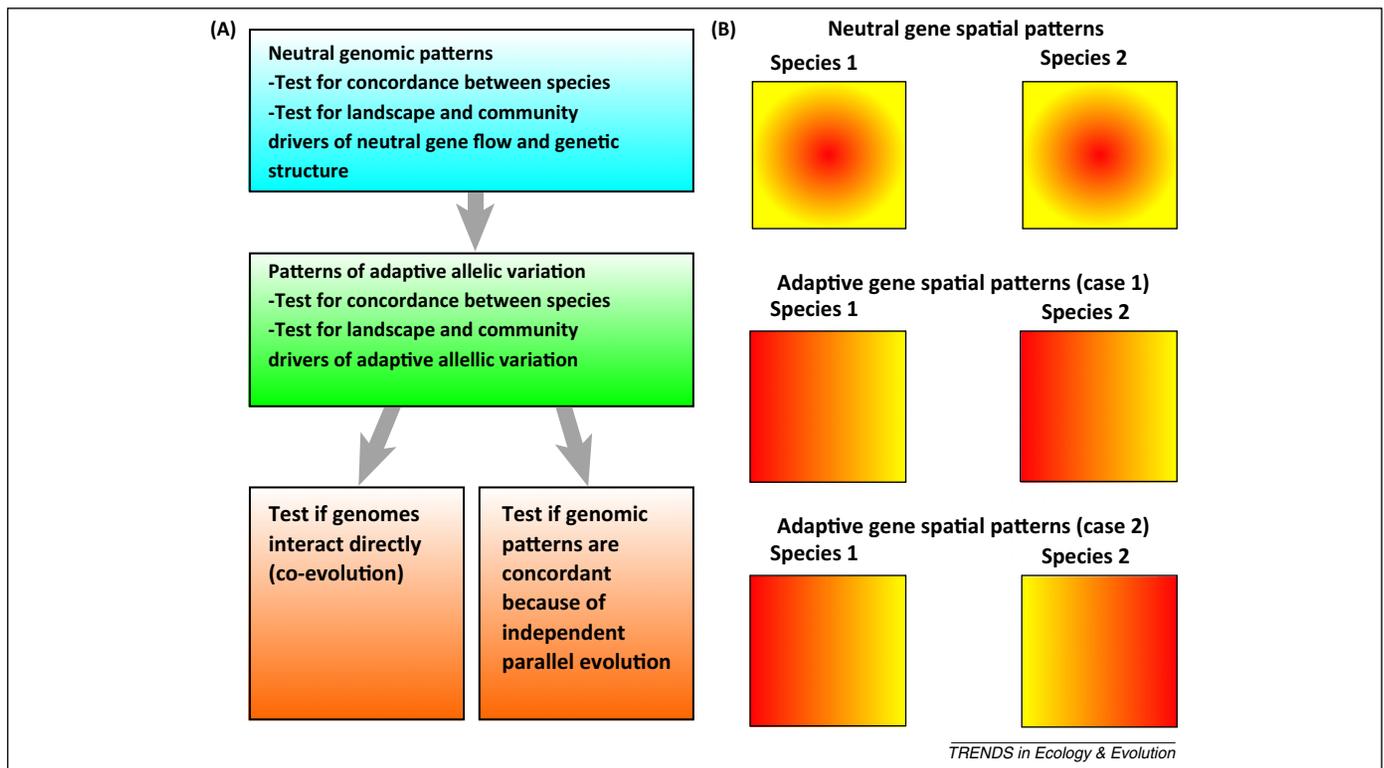


Figure 1. Conceptual components of the landscape community genomics (LCG) approach. **(A)** Describes a general workflow for how a LCG approach might proceed. **(B)** Represents potential neutral and adaptive allele frequencies across hypothetical landscapes, and highlights how patterns of inter-specific genetic variation can vary or interact depending on the direction of biotic or abiotic selective pressures. For example, patterns of neutral genetic variation might be similar in different species, while adaptive genetic variation can simultaneously demonstrate spatial patterns that are distinct from neutral processes, and that are either similar (case 1) or contrasting (case 2) between species. In case 1, adaptive genetic variation could be similar in different species because of co-evolution (e.g., co-adaptation) or independent parallel evolution. In case 2, different patterns in adaptive genetic variation can result from species-specific responses to the local abiotic environment, inter-specific interactions (e.g., predation), or even complex interactions between local abiotic conditions and species interactions (i.e., context-dependent interactions). The key challenge for LCG – and for that matter any landscape or community genetic study – is to identify the degree to which biotic and abiotic drivers influence neutral and adaptive genetic variation; this challenge will likely require replicate sampling in variable environments where focal species exist in sympatry and allopatry.

patterns of population genetic variation in interacting species, there are relatively few empirical examples.

Similarly, community genetics lacks consideration of important spatial and environmental processes, and generally focuses on how a single foundational (or keystone) species shapes the evolution of other members of the local community [18]. There is a growing body of empirical evidence that species interactions (e.g., mutualism, competition, predation, hybridization, disease spread, etc.) are context-dependent, with significant variation in the strength of species interactions and resulting patterns of coexistence along spatial and abiotic gradients [19,20]. For example, ecological and evolutionary interactions among stream-dwelling salmonids are highly context-dependent and can be driven by variation in abiotic and biotic factors over time and space [12,21]. Climate (e.g., temperature) can play a key role in host–pathogen interaction and the spread of disease [22], and third-party interactions (e.g., plant–soil microbial communities) can enhance competition of an invasive plant species by way of a growth-enhancing bacteria [23]. Clearly, context-dependent interactions occur across diverse trophic levels and taxa, but how context-dependent interactions intensify or buffer the effects of species interactions on genomic variation is poorly understood [19].

What is LCG?

LCG is the study of how neutral and adaptive genomic variation within and among populations of interacting species is shaped by both abiotic and biotic factors across diverse landscapes. LCG is distinct from other approaches in that it explicitly tests whether patterns of genomic variation in multiple species vary as a result of inter-specific interactions and whether these interactions vary across landscape or environmental gradients. In other words, LCG attempts to quantify the effects of eco-evolutionary processes occurring across complex environments where selective pressures, gene flow, and genetic drift interact in time and space. This includes genome \times genome interactions (e.g., hybridization, antagonistic or mutualistic co-evolution, etc.), genome \times environment interactions (e.g., parallel adaptation, demography, dispersal, etc.) and, ultimately, genome \times genome \times environment interactions (e.g., context-dependent interactions among species) that shape the patterns of neutral and adaptive genetic variation.

LCG brings together a rich history of approaches in genetics and ecology, including foundations in population genetics, landscape ecology, and community ecology (Figure 2). With such a robust theoretical foundation, the recent explosion in genomic sequencing could prove to be the necessary catalyst in unraveling the complex interactions of geography, ecology, and evolution shaping the genomes of entire communities of species [24–26], thus opening the curtain on a new and exciting act in the evolutionary play.

What types of data and sampling are useful in LCG?

LCG studies focus on multiple interacting species distributed along landscape or environmental gradients. Fundamentally, these studies require three distinct datasets: genomic data on the focal species, ecological data on those species (e.g., occurrence, abundance), and environmental data across the study area. Even with these data,

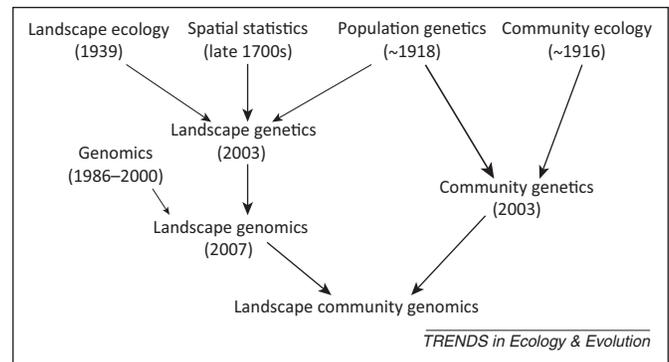


Figure 2 A perspective timeline describing the origins of landscape community genomics (LCG). LCG melds the rich history of genetics and ecology, including foundations in population genetics, landscape ecology, and community ecology. Arrows point to the conceptual progression through time from each main discipline to the corresponding sub-discipline. In parentheses are the approximate dates that each discipline or approach was established [4,5,62–67].

landscape level eco-evolutionary dynamics are challenging to causally attribute to key biotic interactions or environmental conditions because both species interactions and environmental conditions vary spatially and temporally (e.g., context-dependence or environmental gradients). Partly, the solution requires capitalizing on genetic and ecological data sources (e.g., measures of demographic connectivity to complement measures of genetic connectivity [27]), but it also requires strategic sampling across abiotic and biotic conditions.

Ideally, ecological and environmental data – the independent variables in LCG models – should be spatially (and if possible, temporally) diverse to capture strong environmental gradients and key moments in community structure and function (e.g., before and after a disturbance event, introduction of an invasive species, or colonization of novel habitat). Replication across biotic and abiotic gradients is crucial to correctly identify drivers of genomic diversity because community composition is also a direct result of environmental processes, thus further complicating our ability to correctly identify the sources of abiotic and biotic variation influencing genomic diversity. Often, this will require combining genomics data (individual, population, and community level) with modeled or remotely sensed climatic and landscape data to identify environmental drivers of genomic variation and fine-scale data on community composition, abundance, or occurrence patterns of interacting species. Gathering the necessary fine-scale data is not trivial, and this might partially explain the emphasis on geographic and abiotic variables in most landscape genetic studies. However, these data are crucial to advance understanding of how landscape \times community interactions shape genomic variation within and among species.

Furthermore, the LCG approach requires the identification of candidate adaptive genes controlling local adaptation in the focal species, preferably with known or potential effects on species interactions [28]. Future research can capitalize on recent genomic advances that are key to the emerging field of LCG, and are providing unprecedented opportunities to study genome-wide markers under selection in multiple non-model species (rather than focusing on specific questions genomics can answer, we

instead refer readers to excellent, recent publications that give greater details on the use of the following techniques in practice [6,24,25,29]. Novel exon-capture techniques, for example, target areas in or near genes of known or suspected function, allowing capture of neutral and adaptive gene markers [30]. Targeted sequencing of exons is also useful for LCG because multiple divergent species can be sequenced for the same exons [30,31]. Various forms of RAD sequencing (restriction site-associated DNA sequencing) can be applied to any non-model species because it requires no genomic resources [29]. A relatively inexpensive version of RAD-seq is targeted capture of thousands of informative (highly polymorphic) RAD loci, and this can cut costs and thereby facilitate multispecies LCG studies [24]. Finally, metagenomic techniques are potentially a useful genetic technology for LCG-type studies in the future because these techniques offer the ability to yield DNA sequences for multiple species simultaneously [32].

LCG can answer previously intractable questions in eco-evolutionary biology

The emerging LCG perspective and approach can help to address previously confounded and intractable questions in community ecology and evolutionary biology. To illustrate this we use examples from a range of taxa and sub-disciplines, including examples from conservation genetics and community co-evolution. Finally, we discuss a common conceptual gap in current studies that underscores the importance of the LCG approach: the influence of community dynamics on gene flow.

Accounting for evolution in conservation and management

LCG offers a new dimension in conservation management by broadening our understanding of how current and future change might impact upon evolutionary processes at the community and ecosystem scales. Maintaining populations and their adaptive potential requires preservation of life-history variation, connectivity corridors among populations, and genetic variation within and among populations. Thus, most conservation strategies have focused on reducing vulnerability (i.e., sensitivity and exposure) to climate and human stressors, increasing adaptive capacity (i.e., resiliency), and anticipating and facilitating ecological transitions (e.g., range-shifts and resulting species addition or loss) that are caused by the changing environmental conditions [33].

Clearly, genetic data are valuable for advancing our understanding of species and community vulnerability to local environmental conditions, and shifts in those conditions, but there are very few instances where genetic data have been used in this context, especially for multiple interacting taxa. Genetic structure and diversity represent species' sensitivity and adaptive capacity, both of which are key elements of assessing vulnerability of populations [34]. The more-holistic approach offered by LCG can better inform vulnerability assessments over large, ecologically diverse landscapes, which is increasingly important for conservation efforts that seek to increase resiliency in natural ecosystems, maintain important eco-evolutionary dynamics, and avoid biodiversity loss.

LCG can also offer insight into eco-evolutionary relationships among native and non-native species. For example, hybridization (or the lack thereof) arises from localized interactions between species, but is often viewed as a consequence of co-occurrence alone (i.e., if species occur together and can interbreed, they will), which places the emphasis on abiotic and spatial predictors of co-occurrence. However, similarly to other ecological interactions, the localized interactions that promote or prevent hybridization are context-dependent. There is growing evidence that hybridization dynamics can be influenced by interactions between community and environmental sources of selection, ultimately resulting in complex patterns of genetic admixture and adaptive evolution [11,35]. LCG gives us the framework in which to identify how abiotic and biotic drivers affect hybridization rates among species whether naturally sympatric or allopatric (Box 1). Adaptive introgression, for example, has been shown to counteract anthropogenic habitat change (e.g., the use of insecticide to control mosquito vectors of malaria was counteracted by introgression of insecticide-resistance genes from one mosquito species into another) [36]. Adaptive introgression is also of interest because of the role it plays in shaping genome-wide patterns of invasive admixture in species of conservation concern (Box 1) [11,37]. Additional work will be necessary to describe the role of biotic and abiotic interactions affecting dynamics of adaptive or maladaptive introgression, or how introgression can influence other eco-evolutionary dynamics such as dispersal.

Communities as co-evolving units

The LCG framework is necessary to quantitatively test complex community versus environmental interactions in co-evolving communities. Currently, relatively few examples of this quantitative approach exist in the community genetics and landscape genetics literature. Community genetic studies can be further improved by testing whether

Box 1. LCG case study 1: the impact of climate on hybridization and introgression

LCG approaches were used to understand how interactions between landscape features, climatic gradients and change, invasion dynamics, and natural selection influenced introgression between a native (*Oncorhynchus clarkii lewisii*) and non-native (*Oncorhynchus mykiss*) trout. Landscape features, namely stream gradient and elevation, appear to play a role in influencing introgression across space [68], but interactions between precipitation (a surrogate for stream flow) – across space and climate-induced changes over time – as well as distance to the source of the *O. mykiss*, strongly explained spatiotemporal variation in introgression, with recent climatic change facilitating invasive hybridization [12]. This is particularly concerning because selection, in general, appears to strongly favor the native taxa [69]. Nevertheless, subsequent genome-wide scans have identified superinvasive genes from the non-native *O. mykiss* that might have been driven to high frequency by natural selection [37]. Thus, some non-native genes are invading the native genome (gene pool) despite strong genome-wide selection against *O. mykiss* (outbreeding depression [70]). That is, some non-native genes might be selected for (depending on the environment), while most non-native genes are selected against. Given the strong role of climate in influencing introgression between these fish, climate change is likely to play a crucial role in determining future patterns of neutral and adaptive introgression between these species.

spatiotemporal patterns of environmental variation change the strength or pattern of genetic structure that foundation species impose on local communities [18]. In the case of co-evolution between humans and dairy cattle,

adaptive and neutral markers were necessary to illuminate specific patterns of genetic structure driven by farming (Box 2) [38]. Recent landscape genetics studies have adopted multi-species approaches to test hypotheses

Box 2. LCG case study 2: gene–culture co-evolution in humans and cattle

The LCG approach can provide mechanistic insight on co-evolutionary dynamics by combining neutral and adaptive gene markers from multiple interacting species across strong spatiotemporal selection gradients, then testing for interactions between species, genomes, and the environment (see Figure 2 in main text). Cultural co-evolution drove the correlated spatial genetic structuring of neutral and adaptive (selected) genes in both cattle (*Bos taurus*) and humans across Europe [38] (see Figure 1). Genes associated with milk production in cattle [α S1-casein (*CSN1S1*), β -casein (*CSN2*), α S2-casein (*CSN1S2*), κ -casein (*CSN3*), β -lactoglobulin (*LGB*), and α -lactalbumin (*LAA*)], and the lactase

persistence allele in humans, have strikingly similar spatial patterns across Europe [38] (GenBank accession numbers for the cattle milk genes: X59856, X14711, M94327, X14908, X14719, AF249896). However, neutral genetic markers in both species show a different spatial pattern from milk genes, and suggest a similar demographic movement (or colonization) pattern from the Fertile Crescent area across Europe. These types of multi-species genomic approaches are increasingly feasible using massively-parallel sequencing that allows assessment of both neutral and adaptive gene markers in interacting species sampled through time and space (e.g., across complex landscapes).

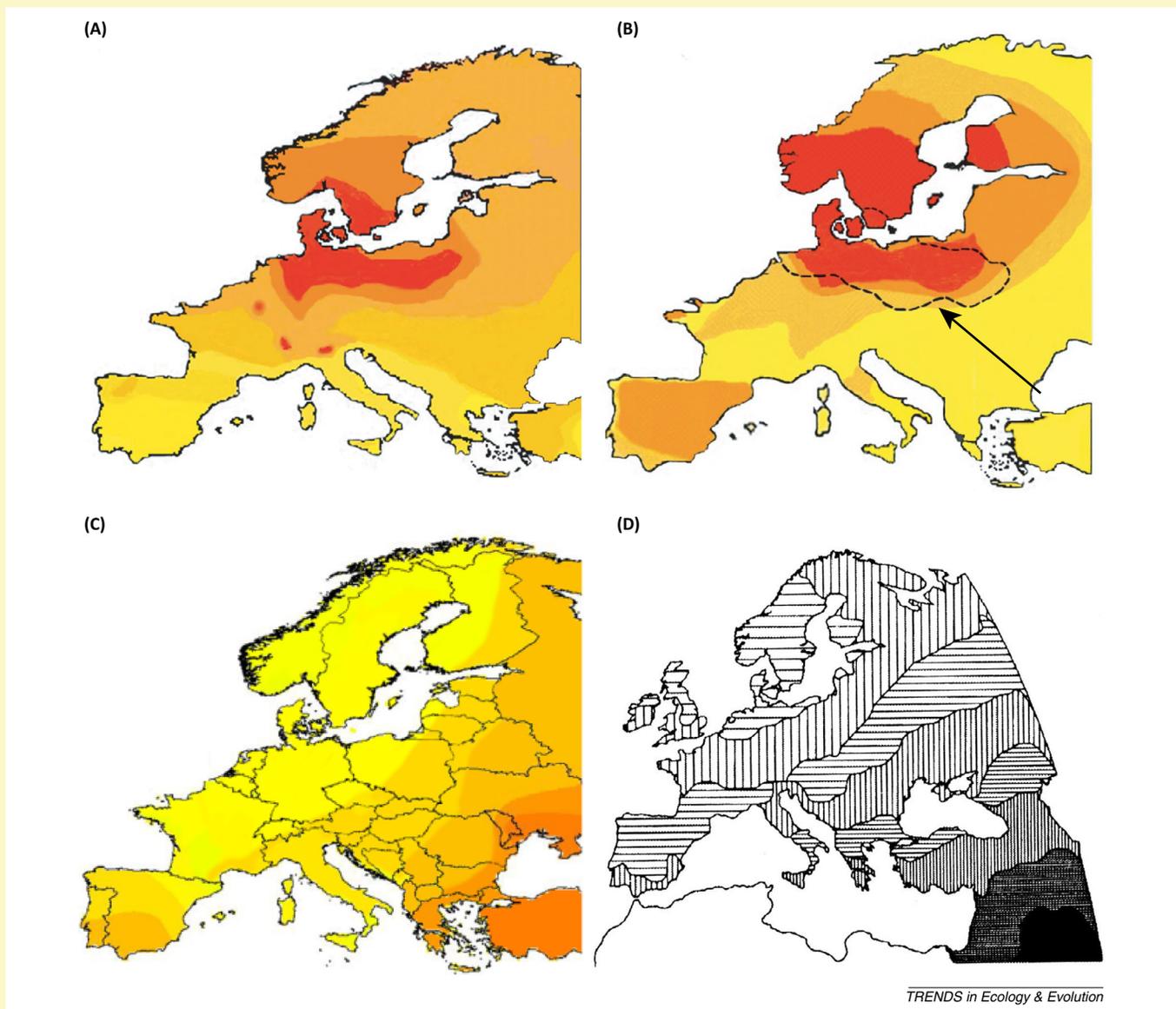


Figure 1. Co-evolution drove the spatial genetic structuring of milk gene diversity in cattle and humans across Europe. This co-evolution could not have been uncovered or fully understood without a landscape community genomics (LCG) approach using both neutral and adaptive gene markers in the cattle and humans (together with an understanding of spatiotemporal cultural differences). The four synthetic maps show genetic spatial variation at (A) the six most important milk genes in cattle, and (B) the lactase persistence allele (allowing milk digestion) in humans [38]. The broken black line (see arrow) in panel (B) indicates the limits of the geographic distribution of early Neolithic milk cow pastoralists inferred from archaeological data (e.g., milk residues in pottery). Panels (C,D) are neutral patterns of genetic diversity showing a cline or gradient across Europe originating in the Fertile Crescent (Iraq, Iran, and Syria) for cattle and humans, respectively. Image credits: panels A and B are reproduced, with permission, from [38], ©2003 Macmillan Publishers Ltd, panel C is an unpublished figure using published data [71], and panel D is reproduced, with permission, from [72], ©1994 Princeton University Press.

across species and landscapes, but without considering the effects of local community composition or landscape \times community interactions [8,39,40]. We believe it is crucial that future studies start to consider LCG perspectives to explicitly test hypotheses of the effects of community (species) interactions on genetic structure within and between populations and environments.

At some level, metagenomics already embodies the LCG perspective and approach by elucidating variation in microbial community structure and distribution across abiotic gradients (e.g., temperature and pH) [41]. Overall, metagenomics is pioneering new ways of thinking about microbial (multi-species) systems, where communities are becoming the units of evolutionary and ecological study among bacteria, archaea, protists, and fungi [13]. Metagenomic approaches can be combined with higher-resolution genome-wide techniques (e.g., exon capture or RAD-seq) to study diversity within and between a wider range of taxa. Overall, these combined techniques could be used to identify important broad spatiotemporal interactions between microbial, plant, invertebrate, and even vertebrate species. For example, in conservation monitoring, this combined approach could be used to test if the arrival of an invasive species causes changes in the evolutionary dynamics of native communities, especially gene diversity and gene flow, or if the strength of the changes is influenced by differences in local environment [42].

Community dynamics affect gene flow

In the past decade, ecologists have shown renewed interest in how dispersal affects the patterns of species coexistence and biodiversity. In particular, both the influential neutral theory of biodiversity [43] and metacommunity theory [44] emphasize the importance of understanding dispersal rates to explain species coexistence in local communities. This body of theory focuses primarily on the demographic effects of dispersal – as a subsidy to local populations that prevents competitive exclusion. In metacommunity theory there has been some effort to incorporate the genetic effects of dispersal (i.e., gene flow) on competitive interactions [45]. However, the LCG framework offers tremendous potential for exploring eco-evolutionary interactions among dispersal, gene flow, and species interactions, and, more broadly, for exploring the underlying abiotic and biotic drivers of dispersal evolution.

The LCG framework incorporates species interactions in analyses of genomic variation in complex landscapes. Competitive asymmetries among co-occurring species are known to influence rates of emigration and immigration in local communities [46], leading to different rates of gene flow in competitively dominant and inferior species [47]. Thus, not only can competitive interactions play a central role in landscape-level patterns of genetic structure, but they also set the stage for evolutionary feedbacks between gene flow and local ecological interactions [48]. In competitively inferior species, high gene flow might constrain incremental evolution of locally adapted competitive traits, while increasing the probability of adaptation to novel conditions by maintaining high levels of standing genetic diversity [49,50]. In competitively dominant species, low rates of gene flow might promote incremental

competitive evolution, whereas standing genetic diversity should be reduced relative to the competitively inferior species, constraining evolutionary responses to novel selective forces.

These and other evolutionary processes (e.g., spread of novel mutations, heterozygote advantage) could easily be missed with traditional landscape genetics methods that focus on geographic or habitat-related effects on gene flow [51]. Unraveling geographic, ecological, and evolutionary effects on landscape genetics relies on the combination of neutral and non-neutral markers provided by genomics data, as well as on the multi-species and multi-factorial LCG approach (Figure 1). Great advances could be made simply by accounting for community composition in landscape genetic models, allowing local biotic effects to compete with habitat and geographic effects in statistical models [52,53]. Further, it is possible to discern local adaptation (e.g., in a competitive dominant) by comparing patterns of genetic structure of neutral and non-neutral markers, and by testing for patch-specific effects (biotic or abiotic) on genetic structure.

In addition to advancing understanding of how ecological dynamics influence spatial patterns of genomic variation, the LCG framework is ideal for testing hypotheses for the evolution of dispersal – one of the most challenging areas of research in ecology and evolution [16,54]. The most broadly applicable hypothesis predicts that dispersal is maintained by spatial and temporal variability in the quality of local habitat patches [55–57]: temporal variability promotes movement away from an initial location; spatial variability creates the possibility that dispersal will be rewarded with increased fitness. A few empirical studies support this hypothesis (e.g., [57,58]), but empirical tests have been impeded by the difficulty of linking variation in individual fitness (e.g., between dispersers and non-dispersers) to spatiotemporal variation in specific components of local habitat quality (e.g., interspecific competitive effects [59] vs abiotic conditions [60]).

The LCG approach offers a way forward by providing a conceptual framework for integrating information on patch geography (e.g., inter-patch distance), species composition and abiotic conditions within patches, and the spatial structure of neutral and non-neutral loci. Specifically, the habitat quality hypothesis would predict that rates of neutral gene flow should increase with spatiotemporal variation in key components of local habitat quality (biotic vs abiotic), after correcting for patch geography. In addition, spatiotemporal patterns in non-neutral loci can provide insight on the specific dispersal traits under selection [61].

Concluding remarks

Landscape genetics and community genetics have developed as largely-independent disciplines, growing in popularity and importance, but without capitalizing on the complementary nature of the two approaches. Intuitively, however, we know that natural systems comprise multiple species that interact and exist in highly-variable abiotic environments. We believe that combining landscape and community genetics approaches and perspectives is crucial to illuminating the factors driving eco-evolutionary processes occurring within ecosystems and across landscapes.

The recent explosion in genomic sequencing and genotyping techniques – applicable to any species – will help biologists to exploit the enormous potential of LCG approaches. Not only does the LCG approach and perspective represent an exciting frontier in the integration of basic evolutionary and ecological research, but it is also a crucial tool for understanding how interrelated and accelerating rates of biodiversity loss and global environmental change will affect the evolutionary trajectory of species and natural communities.

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