



Where's the ecology in molecular ecology?

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Molecular techniques have had a profound impact in biology. Major disciplines, including evolutionary biology, now consistently utilize molecular tools. In contrast, molecular techniques have had a more limited impact in ecology. This discrepancy is surprising. Here, we describe the unexpected paucity of ecological research in the field colloquially referred to as 'molecular ecology.' Publications over the past 15 years from the journals *Ecology*, *Evolution* and *Molecular Ecology* reveal that much of the research published under the molecular ecology banner is in fact evolutionary in nature, and that comparatively little ecological research incorporates molecular tools. This failure to more broadly utilize molecular techniques in ecology is alarming because several promising lines of ecological inquiry could benefit from molecular approaches. Here we summarize the use of molecular tools in ecology and evolution, and suggest several ways to renew the ecological focus in 'molecular ecology'.

Progress in science is almost always shaped by the tools available to its practitioners. Microscopes, computers, and several other technological advances have profoundly influenced the way modern scientists form and attempt to answer their most fundamental questions (Burke et al. 1992, Queller et al. 1993, Amos 2000). Interestingly, once research tools become commonplace, alternatives to common application of these tools are frequently resisted (Kuhn 1962, Hung 2006). Over the past three decades molecular genetic techniques have become increasingly important to biologists, particularly as the variety of molecular tools has increased. However, the utilization of molecular techniques varies greatly among biological disciplines. Nowhere is this discrepancy more pronounced than between the fields of evolutionary biology and ecology. Molecular approaches now pervade evolutionary biology: indeed, some evolutionary disciplines are almost completely bound to molecular approaches (e.g. phylogenetic systematics and phylogeography). In contrast, several disciplines in ecology have largely passed over molecular techniques, even where the utilization of molecular approaches could help solve some of our most interesting ecological problems.

The current molecular divide between ecology and evolution is puzzling. Although certain lines of ecological inquiry appear to be better suited than others to the use of molecular approaches, we are convinced that more attention focused by ecologists on the incorporation of molecular techniques could enhance ecological research. Here, we remind readers of the original breadth of the field of 'molecular ecology' and demonstrate how this field has become unexpectedly specialized, drifting away from a general ecological emphasis and toward a more narrow

phylogenetic one where molecular markers serve primarily as historical tracers. We argue for a renewed effort to restore the ecological component of molecular ecology, and we demonstrate the potential value of this shift by pointing to some fundamental questions in ecology that could benefit from a molecular perspective.

The misnomer of molecular ecology

Quantifying the use of molecular techniques in ecology and evolutionary biology can tell us a great deal about how the field of molecular ecology has developed since its inception. What we really want to know is the degree to which modern molecular ecology addresses ecological problems versus evolutionary problems. However, this first requires delineating disciplinary boundaries between ecology and evolution. These are typically viewed as allied fields, often complementary in their findings, but from our perspective clearly distinct in focus. Whereas ecology examines patterns and processes that underpin the distribution and abundance of organisms in their environments (Ricklefs and Miller 1999), evolutionary biology explores how characteristics of populations change through space and time, including understanding the role of environmental and genetic factors in shaping patterns of biodiversity (Futuyma 2005). Hence, we can use these broad definitions to explore the application of molecular methods in each discipline.

Intuitively, the term 'molecular ecology' could cast a net over any focal area in ecology where molecular tools are used to address fundamental ecological questions. However, there is a growing feeling among ecologists that most current research being conducted under the molecular

ecology banner is not ecological in nature. Rather, contemporary molecular ecology is viewed as being concerned largely with the evolutionary field of phylogeography. This bias may be due to several factors, but there is a growing perception that modern molecular ecology has little to do with fundamental ecological problems. This idea is reinforced by the sense that many studies published in journals dedicated to molecular ecology are evolutionary in focus, and that there are few molecular-based studies on ecological problems being published in core ecological journals. Here, we explore the validity of these perceptions. We ask: where is the ecology in the field of molecular ecology?

To address this question we examined the use of molecular tools over the past fifteen years in three representative journals – *Ecology*, *Evolution* and *Molecular Ecology*. As basic journals in their respective fields, these publications are likely to capture the breadth of leading research being conducted in various sub-disciplines of ecology and evolutionary biology. To acquire a quantitative snapshot of the degree to which evolution and ecology utilize molecular tools, we characterized papers published in recent volumes (odd years, 1993–2007). We partitioned these fields into 13 sub-disciplines (Table 1): the first six are ecological fields taken from the major categories used to classify presentations at recent annual meetings of the Ecological Society of America; the remaining seven are evolutionary fields taken from the major categories generally used to classify presentations at the joint society meetings of the Society for the Study of Evolution, the American Society of Naturalists and the Society of Systematic Biologists. We note that some of these sub-disciplines share more overlap than others. For example, population ecology and population genetics both focus on demographic trends, but do so over different time scales. Ambiguous cases in our data set were rare and were resolved based on the context of the questions they sought to answer. We then examined the proportional use of molecular tools in each of these sub-disciplines, measured as the number of papers that used molecular techniques divided by the total number of papers. Papers from all three focal journals from all years were combined, thus providing a broad view of

molecular tool use by discipline. The results are clear: molecular tools are infrequently used in ecology relative to evolutionary biology (Fig. 1). Only behavioral ecology (with a proportion of 0.28) ranked in the upper half of all combined sub-disciplines, while four of the remaining five ecological fields ranked at the bottom of all sub-disciplines. Interestingly, three evolutionary fields – phylogeography, systematics and speciation – actually used molecular tools in the majority of their published papers.

We also examined the trends of molecular tool use over time in both ecology and evolutionary biology (Fig. 2). Again, we combined publications from all three journals; we also combined sub-disciplines, allowing us to compare the two broad categories of ecology versus evolutionary biology. We found that the use of molecular tools in these two fields has remained relatively constant in proportion over time, with a modest increase in both fields in 2005 followed by a slight decrease in 2007. Overall, ecological studies incorporate molecular tools at a proportion of 0.12; evolutionary studies do so at a proportion of 0.55. Hence, it appears that the lack of molecular tool use in ecology is not simply due to insufficient time for these techniques to ‘catch on’.

Finally, we examined which of the three focal journals were most likely to publish molecular-based ecological studies and which were mostly likely to publish molecular-based evolutionary studies (Fig. 3). Not surprisingly, most of the articles published in the journal *Ecology* were ecological in nature and most in the journal *Evolution* address evolutionary problems, although some cross publishing occurs. What was surprising is just how few of the ecological papers published in *Ecology* used molecular tools; in fact, ecological studies published in the journal *Evolution*

Table 1. Ecology and evolutionary biology sub-disciplines. Sub-disciplines were generated from categories used to classify presentations at annual meetings of the Ecological Society of America and joint meetings of the Society for the Study of Evolution, American Society of Naturalists and Society of Systematic Biologists.

Ecology

1. Behavioral ecology
2. Population interactions
3. Evolutionary ecology
4. Demography/population dynamics
5. Macroecology
6. Community ecology

Evolution

7. Phylogeography/biogeography
8. Phylogenetic systematics
9. Speciation
10. Quantitative genetics
11. Coevolution
12. Macroevolution
13. Adaptation

Use of molecular tools by discipline

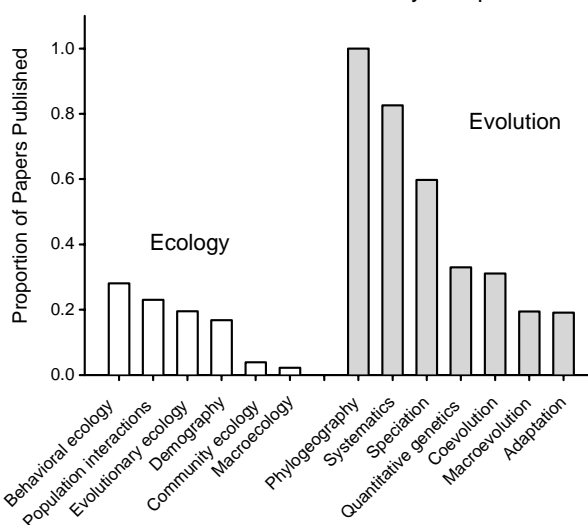


Figure 1. Summary of molecular tool use across 13 sub-disciplines of ecology and evolution measured as the proportion of papers published that used molecular methods. Our data are based on the use of molecular techniques in papers published over the past 15 years (1993–2007) combined across three representative journals. Open bars are ecological fields; shaded bars are evolutionary fields. See text for details on how these sub-disciplines were chosen, and which journals were used.

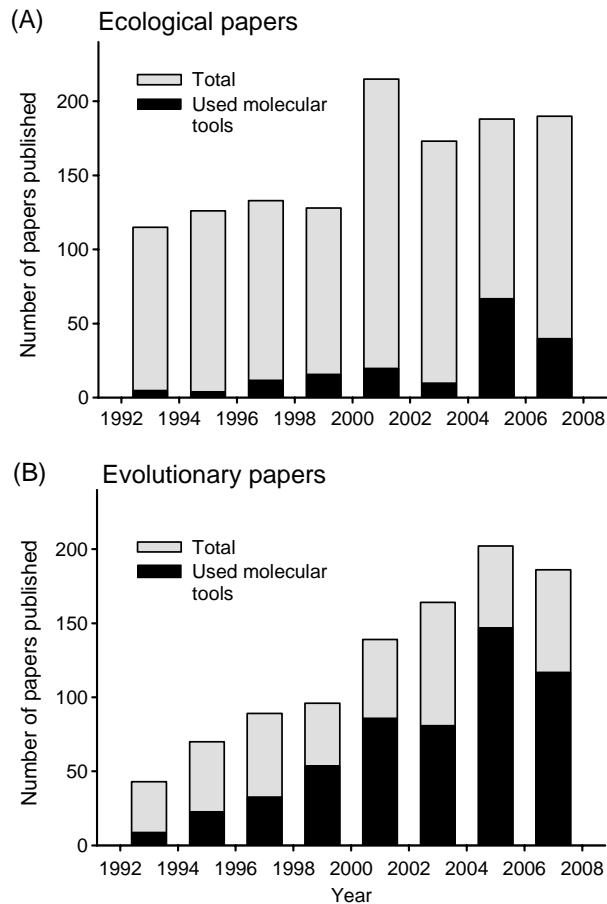


Figure 2. Trends in molecular tool use over time in the fields of (A) ecology and (B) evolutionary biology based on publications from three representative journals. Sub-disciplines in these two fields are combined. Data are shown for odd years from 1993 to 2007. Gray shaded bars indicate the total number of papers published (combined across journals) and solid black bars show the number of those papers that used molecular tools.

were much more likely to use molecular tools than those published in *Ecology*. We were also intrigued to find that the majority of papers published in the journal *Molecular Ecology* were evolutionary studies, not ecological. Hence, even the namesake journal *Molecular Ecology* suffers to some extent from the lack of incorporation of molecular methods in the field of ecology, despite the longstanding call for such papers in the journal (Burke et al. 1992, Rieseberg and Smith 2000a, 2000b, 2001, Purugganan and Gibson 2003).

The unfulfilled promise of molecular ecology

The patterns revealed here are quite different from the expectations of molecular ecology as a field when it was conceived over a decade ago. As the discipline began to take form through the 1980s and early 1990s several researchers debated exactly what molecular ecology might encompass (Burke et al. 1992, Beebe and Rowe 2004). At one extreme were scientists who held that molecular ecology should be very flexible in the types of problems it addressed, essentially leaving room for any study that

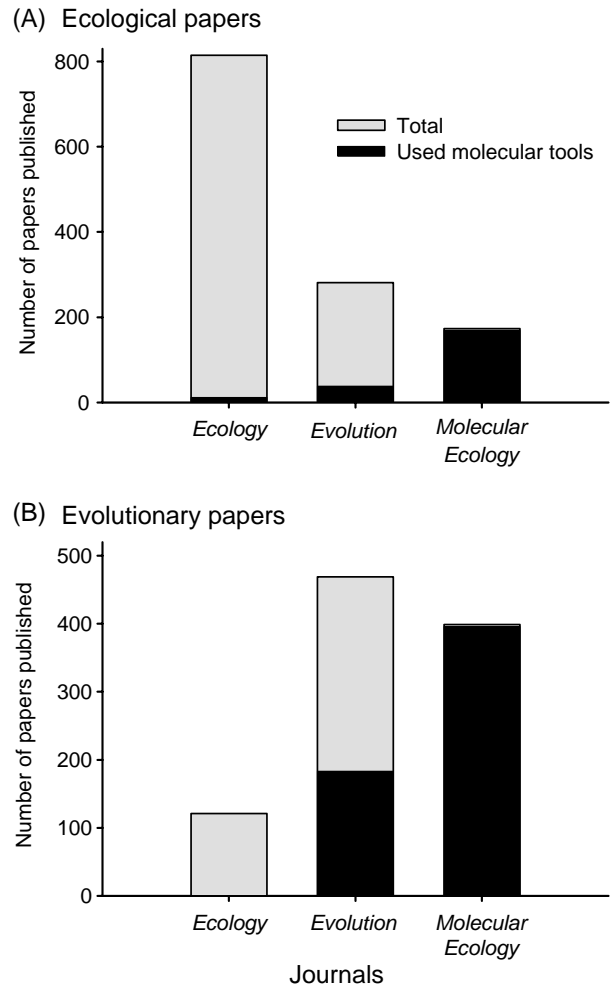


Figure 3. The number of papers published in the journals *Ecology*, *Evolution* and *Molecular Ecology* summed across odd years (1993 to 2007) and separated into the disciplines of (A) ecology and (B) evolutionary biology. Gray shaded bars indicate the total number of papers published by journal and solid black bars show the number of those papers that used molecular tools.

applied molecular genetic methods to problems in the natural environment. At another extreme were scientists interested in understanding how molecular genetics could be used to address traditional ecological problems (Burke et al. 1992). With the former paradigm, molecular markers defined the field; under the latter paradigm, ecological questions had primacy.

Exactly what kinds of ecological questions did molecular ecology promise to answer? Several starts were made – some have materialized, many have not. Some of the earliest incarnations of molecular ecology as a field focused on conservation problems. For example, many ecologists expected molecular markers to provide insight into how invasive species or genetically modified organisms released to natural environments would affect local population dynamics and community organization (Sakai et al. 2001). Many also foresaw the benefit of using molecular markers to define conservation unit boundaries. Yet the focus of this work for several years was on genetic delineation (Moritz 1994) while failing to incorporate ecological elements to define conservation units (but see

Ryder 1986, Waples 1991), an omission only recently reconsidered in the conservation unit literature (Crandall et al. 2000). Perhaps the most prominent expectation of molecular ecology was that molecular techniques could be used to provide a historical perspective on ecological processes. This so-called 'historical ecology' called on cladistic methods – now based mostly on molecular data – to offer a phylogenetic perspective on ways that organisms interact with their environments (Brooks and McLennan 1991, 2002). Recent work combining environmental niche modeling with phylogeography attempts to understand contemporary species distributions in light of habitat constraints (Lapointe and Rissler 2005, Victoriano et al. 2008). Researchers also expected molecular ecology to tell us something about historical patterns of community assembly (Avice et al. 1987). Finally, molecular methods were expected to have a major impact on behavioral ecology, primarily through DNA fingerprinting approaches applied to the identification of individual organisms; the most prominent use in this field being the assignment of paternity or maternity (Ross 2001). Wildlife ecologists in particular used molecular methods to amplify DNA from field-samples of hair and feces to identify individual organisms (Piggott and Taylor 2003, Walker et al. 2006) providing insight into animal movement patterns (Walker et al. 2006) and foraging behavior (Farrell et al. 2000, Fedriani and Kohn 2001), and to generate estimates of population size (Kohn et al. 1999, Mills et al. 2000).

From these early starts in molecular ecology emerged an even more ambitious objective: to identify the genetic basis for individual phenotypic traits that ultimately shape population-level ecological processes (Conner and Hartl 2004, Lowe et al. 2004). The legacy of this effort to understand the genetics of phenotypic expression and its ecological consequences remains a key focus of modern ecological genetics, albeit an elusive one. Molecular-based techniques, such as quantitative trait loci (QTL) and genomic microarray assays, provide rudimentary insight into the genetic basis of some phenotypic traits. However, explaining community level patterns in nature from a genetic perspective remains an unfulfilled promise of molecular ecology, yet one of particular importance. Current progress in the field of genomics holds great potential for revealing the ultimate explanations for why organisms are distributed as they are in both space and time – this is an exciting prospect for ecology.

Molecular methods to solve ecological questions

Some ecological disciplines have made greater use of molecular tools than others, yet common use of molecular approaches is not evident in any ecological field (Fig. 1). Several arguments can be made to explain this pattern. It is possible that some ecological disciplines are slow to make use of molecular tools because important questions in these fields can be answered adequately without molecular approaches. It is also possible that the widespread use of molecular tools as historical tracers – that is, tools to reconstruct historical patterns – gives the impression that they are of limited use for contemporary ecological questions. Alternatively, ecologists may simply be slow or

unwilling to adopt new tools that are perceived to be the domain of molecular biologists (what some refer to as a 'gel jockey' syndrome). One way to examine these possibilities is to ask how well ecologists are answering their most fundamental questions, with or without molecular approaches. We contend that at least in some ecological fields, traditional approaches are reaching the limits of their explanatory power, and that it would be beneficial to integrate new cross-disciplinary approaches. Molecular tools, coupled with synthetic analytical approaches, should be able to help us make new progress on several key ecological questions, including those at the interface of ecology and other disciplines.

What then are the most pressing problems in ecology, and how can molecular techniques help resolve them? In 1999, Robert May outlined several unanswered questions in ecology, focusing specifically on those that were expected to guide the ecological research agenda of the 21st century (May 1999). Several of these questions remain untapped. Interestingly, many of them could benefit from a molecular perspective. We list a subset of May's questions here and briefly point to ways that molecular methods might be incorporated to help gain additional insights. Our list is by no means exhaustive, but should illustrate how molecular techniques might help address some current questions in ecological research, both from a contemporary and historical perspective.

What determines population density and population persistence?

Ecologists have long focused on variation in organismal life histories and their demographic consequences to explain density and population persistence. The use of molecular methods to reveal the genetic underpinnings of complex life histories offers an important way of identifying the relative contributions of life history adaptations versus environmental factors in driving demographic trends. For example, genetic analyses of aging in *Caenorhabditis elegans* reveals that although the genotype is largely responsible for the mean life span of a metapopulation, individual longevity is largely influenced by stochastic environmental effects (Chen et al. 2006, Antebi 2007, Caswell-Chen and Caswell 2007). A functional genomic RNAi screen revealed over 80 genes in *C. elegans* that, when knocked down, result in significant increases in lifespan (Hamilton et al. 2005). It is suspected that many of these genes are pleiotropic (like *daf-2* or *clk-1*, which, by equal factors, simultaneously increase lifespan but decrease fecundity), as revealed by genomic analysis showing genetic correlations between life history traits such as egg size, egg number and body mass (Gutteling et al. 2007). Such studies are honing in on the causal mechanisms responsible for life history tradeoffs that ultimately shape demographic trends (Williams 1957, Caswell 2001, Gutteling et al. 2007). Given that many of the genetic pathways involved in fundamental life history traits (such as lifespan) are highly conserved across all eukaryotes (Curran and Ruvkun 2007), genomic approaches are particularly promising in linking life history evolution to demography. As our ability to economically generate full-genome data sets increases, ecologists should be ready to take advantage of these data. Molecular

ecologists must assume the critical role of linking assays of individual genetic variation to demographic trends.

Molecular methods can also be used to approach the question of population density and persistence from a historical perspective. For example, several analytical methods are now available that use gene trees and genetic diversity data to infer historical population sizes through space and time (Kuhner et al. 1998, Hayes et al. 2003, Drummond et al. 2005, Minin et al. 2008, Vasco 2008). Combining these data with historical reconstructions of environmental conditions offers an opportunity to explore population abundance and persistence on a much greater temporal and spatial scale – albeit a coarser one – than is typically attempted in contemporary ecological studies. Hence, molecular data can help ecologists gain the benefit of a historical perspective to help shape current hypotheses and experiments.

What role does spatial structure play in regulating population stability?

Since its advent, the evolutionary field of phylogeography has explored spatial relationships among populations. Initial work in this field focused solely on historical patterns of gene flow through space – in ecological terms, this might be viewed simply as the successful movement and reproduction of individuals across a geographic landscape. Hence, phylogeography offers ecologists a way to look back in time and quantify historic patterns of spatial linkages among populations. The issue of population stability can be assessed via historical demography, where researchers are able to infer patterns of population expansion, stability, or bottlenecks through space and time. The current focus in phylogeography is on combining data from several co-distributed species; as multiple data sets become available, molecular ecologists will be able to compare historical demographic trends in highly structured species relative to highly connected ones, and ask if there is any association between spatial structure and population dynamics. Extending this idea, the comparative approach could also be applied to multiple interacting species helping us better understand how communities and ecosystems form and persist over time, an original goal of phylogeography (Avice et al. 1987). Hence, comparative phylogeography could be viewed as one additional tool in community ecology research that seeks to benefit from a historical perspective.

How does biodiversity scale with geographic range and body size?

Most studies of biological diversity are viewed at landscape levels, typically ranging from tens to thousands of kilometers, and most focus on large taxa that are visible to the naked eye. In contrast, we know much less about patterns of diversity for very small organisms, even at very small geographic scales. Do organisms smaller than 1 mm even have community provinces, and if so, are these biogeographies comparable to larger organisms? One difficulty community ecologists have had in working with small organisms is species delimitation and identification at this level. Given that most biological diversity is small (<1 mm), and most small organisms have yet to be described, we currently have a clear understanding

of species distributions for only a small fraction of Earth's species. In such cases, molecular methods and sophisticated statistical tools offer our best approach to species identification, an essential prerequisite to describing levels of biodiversity in micro-organisms (Bohannan and Hughes 2003, Cohan and Perry 2007, Green and Plotkin 2007, Lozupone and Knight 2008). The issue of biodiversity and range size is also best approached using DNA sequence data. In some cases where taxa are thought to be geographically widespread, molecular assays have revealed cryptic diversity, in some cases revealing hidden species (Hebert et al. 2004). In other cases, careful examination with molecular methods have revealed methodological problems with DNA barcoding (Song et al. 2008). Still, in most cases molecular techniques currently provide the best, and sometimes only tool whereby ecologists can assay species geographic boundaries and diversity. More importantly, these tools open up studies of micro-organisms that have previously been difficult for community and landscape ecologists to approach.

How do ecological and geophysical factors regulate ecosystem functioning?

Understanding ecosystem functioning remains one of the final frontiers in ecology primarily because of its scope, which includes understanding the ways in which biotic and abiotic components of ecosystems change over time (Noss 1990, Hooper et al. 2000, 2005, Balvanera et al. 2006). Considerable attention has focused on links between ecological factors – such as species diversity, abundance, and distribution – and the flux of energy and nutrients through ecosystems. Still, little is known about the influence of geochemistry and geophysics as drivers of ecosystem functioning. Molecular methods could play an important role in understanding how ecological and geophysical factors govern ecosystem processes.

It is well known that species richness and the abundance of each species can influence ecosystem functioning (Niklaus et al. 2006, Cornwell et al. 2008, Reed et al. 2008). Understanding the former relies on accurate species identification, an enterprise increasingly dependent on molecular approaches, especially for small organisms (as discussed above). Understanding the latter requires knowledge of the functional role that each species plays in ecosystem processes (such as nutrient cycling) and a way to measure the abundance of each species. Here, molecular biogeochemistry is having a major impact in ecosystem research (Zak et al. 2006). A variety of molecular tools can be used to determine patterns of microbe community composition (e.g. T-RFLP, DGGE, LH-PCR, clone library sequences, and next generation sequencing) and molecular approaches like qPCR and microarrays can be used to rapidly recover species abundance (reviewed by Zak et al. 2006). Similarly, by measuring the expression of functional genes involved in biogeochemical pathways (using RT-PCR), we can actually infer the contributions of each species to overall ecosystem functioning (Zak et al. 2006).

Ecosystem functioning is also affected by the geographic distribution of species. Hence, it is important to determine how ecological and geophysical factors influence species

ranges. Environmental niche modeling coupled with molecular phylogeography (Lapointe and Rissler 2005, Rissler et al. 2006, Rissler and Apodaca 2007) provides a way to understand how geophysical changes (i.e. climate) might affect the distribution of species, which in turn can be used to predict patterns of nutrient cycling. Such an approach could be further improved if we could determine the adaptive responses of species to both short and long-term environmental changes. For example, research programs such as ecological genomics, focusing on physiological adaptation at molecular genetic and gene expression levels, can identify functional environmental responses of organisms to changes in their immediate and longer-term environment. These responses by individual species could then be used to model predictions of geographic distributions under different climate change scenarios. Elucidating species-level gene expression patterns and linking these to environmental stresses is now possible due to recent advances in transcriptome and DNA sequencing technologies, and genomic resources such as the Gene Ontology Consortium (Harris et al. 2008, Rhee et al. 2008) and Kyoto Encyclopedia of Genes and Genomes (Kanehisa and Goto 2000).

Integrating genomics and ecology can present challenges. Researchers must recognize that gene expression studies require controlling for environmental effects as well as ontogenetic effects. Moreover, genomic resources are still primarily available for model organisms and not the species we typically work with in the field (Travers 2007). However, the potential payoff (in terms of scope and scale of the ecological problems addressed) reinforces the benefits of pursuing collaborative, multidisciplinary approaches to solving ecological questions, especially as genomic data become available for more species.

Quantifying nutrient cycling of specific elements (e.g. carbon or nitrogen) by different species is also important to understanding ecosystem functioning. The discipline of ecological stoichiometry explicitly links food web interactions to the synthesis of bio-molecules within individuals. Interestingly, the components of this research program that are least explored are also those most empowered by molecular techniques. For example, phosphorus is typically a limiting element in the biosynthesis of rRNA molecules, and the production of rRNA is critical to several traits that impact ecological interactions, including growth and reproduction (Sternler and Elser 2002, Jeyasingh and Weider 2007). Hence, understanding how limited elemental resources are allocated within organisms can tell us a great deal about the role of nutrient cycling on individual traits that ultimately govern ecological interactions. Modern molecular approaches like qPCR can be used to measure the number of copies of rDNA genes, and microarrays can be used to measure the abundance and diversity of rRNA molecules produced from these genes – comparisons can then be readily made among different populations and species over varying environmental gradients to understand the role of limiting resources governing key ecological traits.

Finally, ecologists today are clearly interested in knowing if the effect of climate change on ecosystem functioning is predictable. There is good evidence that changes in the geophysical environment (e.g. temperature, precipitation, etc.) shape the distributions of extant biodiversity (Guralnick

2006), and the distribution of biodiversity in turn impacts ecosystem functioning (Barrett et al. 2004, 2006a, 2006b). Hence, given these known links, we are now positioned to use molecular tools to explore how biogeochemical cycles governed by climate can alter community structure. For example, in a low-diversity polar ecosystem it has been shown that climate-induced changes (over decadal time-scales) can result in altered hydrology, biological productivity, and ultimately community composition (Doran et al. 2002). Recently, Barrett et al. used stable isotope (^{13}C) probes to explore the implications of climate-induced changes on soil invertebrates and carbon cycling. In this particular case, relatively small changes in temperature over a 14-year period altered the soil invertebrate community structure (as determined by genetic barcodes), leading to an estimated 32% loss of function in carbon cycling (Barrett et al. 2008).

Innovative uses of molecular methods in ecology

Although several opportunities exist to expand the reach of molecular ecology, it would be unfair to suggest that ecologists have failed completely to utilize molecular methods. In fact, several recent published examples demonstrate clever ways that molecular tools are now being applied. Here we highlight examples from three ecological sub-disciplines.

Population ecology

Detecting competition and describing its effects are central to several questions in ecology, particularly in trying to understand the causes of extinction. Ecologists often want to understand what happens when biological invasions occur and how one species replaces another. In an innovative study exploring species replacement of one freshwater fish by a closely related species, Moyer and colleagues (Moyer et al. 2005) demonstrate the utility of molecular tools to distinguish between two competing hypotheses: extinction caused by introgressive hybridization versus classical demographic extinction due to competition. Field surveys revealed that over a 10-year time period the fish *Hybognathus amarus* was completely replaced in the Pecos River (New Mexico) by its invading congener *H. placitus*. Microsatellite markers were used to reject the hypothesis that introgressive hybridization was the cause. In a clever extension of the analysis the authors then compared microsatellite allelic diversity between species to estimate the size of the invading population. This estimate, coupled with an estimate of the native fish population size and a set of simulated competition coefficients was used to conclude that species replacement could have occurred by competition within the 10-year window. Hence, molecular tools were used to refute one extinction hypothesis and to evaluate the validity of its alternative.

Community ecology

In some cases, using molecular tools to link disciplines in ecology and evolution can help better address ecological questions. Our literature survey (Fig. 1) reveals that community ecology, as a field, is among the least likely to

employ molecular approaches. In contrast, phylogeography has a long history of using molecular markers as tracers to reveal historical patterns of population distributions. Phylogeography has recently focused on contemporary geographic distributions (Lukoschek et al. 2007, Paun et al. 2008, Ahern et al. 2009). Blending such applications with community ecology enables research on several key ecological questions. How do communities assemble? What links in food webs define and maintain community structure? How do these links change over time? Rather than assuming a common species pool from which current communities have assembled, we can take into account the spatial history of each species in contemporary assemblages. Another promising way of investigating these questions involves changing the way we look at food webs: instead of viewing them as static links that are defined by autecological studies on each of the individual species in the food web, we could consider historical spatial interactions among species in the food web. We consider each of these ideas in turn.

Until recently, linking phylogeography to community ecology was hampered by methodological impediments requiring that the geographic distribution of species comprising communities completely overlap. However, recent methodological advances overcome this problem. For example, Lapointe and Rissler (2005) simultaneously analyzed phylogeographic data sets representing nine co-occurring taxa, each with different ecologies and life history traits. They showed that the distributions of these taxa were shaped by common climate regimes. Broader application of these methods has the potential to address questions regarding community assembly and community stability over time. Similarly, as phylogeographies are reconstructed for each of the species in the food web, they can be linked together to identify shared geographic and evolutionary patterns and infer both historical and contemporary processes. Applying approaches like Lapointe and Rissler (2005) to interacting members of ecological communities effectively reveals a timeline for how the present communities have come to be assembled. Where not all species are present in all communities, this approach also allows for statistical tests of factors that are correlated with physical differences in food web composition, stability (over time) and spatial structure. Thus, comparative phylogeographic analyses of food webs, or trophic phylogeography, can reveal the historical pattern of food web assemblages, and allows for inference as to how stable food webs have been in the past, and perhaps even predict how they might respond to ecological changes in the future.

Behavioral ecology

Traditionally, behavioral ecology is the ecological discipline most likely to use molecular tools (Fig. 1). However, even this field stands to benefit from a broader use of molecular approaches. For example, an exciting new area of behavioral research focuses on behavioral syndromes, the phenomenon of certain kinds of behavioral tendencies to persist across a wide range of social and environmental contexts (Sih et al. 2004). This framework has been used to predict that risk-taking individuals most likely to colonize new habitats are probably not a random sample of the entire group. Rather, the behavioral tendencies that promote exploration and

migration in colonizers might also make these individuals aggressive competitors in their new habitats, providing some additional insight into the nature of invasive species. For example, Dingemanse et al. (2003) showed that in great tits natal dispersal distance is a function of individual personality type, with 'fast-exploring' behavioral types showing greatest dispersal distances. Neutral molecular markers could be used at the population level to test the idea that colonizers are a non-random sample of the source population, and when coupled with assays of behavior could provide new understanding into how behavior shapes ecological interactions, especially at fringes of species' ranges. In fact, molecular methods could be used to test the idea that for some species competitive interactions may be much stronger at their distributional margins.

Conclusions and caveats

A more deliberate application of molecular tools to fundamental ecological problems should prove beneficial. The heretofore-modest application of molecular tools to the full range of ecological problems offers an exciting future for molecular ecology. However, as with any technological advance, it is important to avoid letting molecular tools drive the kinds of questions ecologists ask. Rather, the best science is accomplished when a compelling problem is matched to the most appropriate methods that can be applied to yield an answer. Our point here is that in many cases, important ecological problems – including classical problems focused on the distribution and abundance of organisms – could be better addressed if molecular techniques were employed. The novelty and utility of the approach we advocate also lies in the way these tools can unite disparate sub-disciplines in ecology and evolution to address problems that current research programs alone simply cannot. Solutions to many current ecological questions will require a multidisciplinary approach, and in many cases these approaches could be built upon a molecular framework.

Finally, if molecular ecology is to mature to the point that it regularly addresses ecological problems, it will require ecologists to become facile with molecular techniques. For too long ecologists have believed the false notion that expertise in natural history and experimental ecology is at odds with molecular biology. This attitude has fractured research programs, biological disciplines, and even academic departments for decades, but the fact is that molecular techniques are simply tools. Just as it would be absurd to divide biologists (and their disciplines) into groups that use computers versus those that do not, it is ill-founded to consider molecular techniques as a defining feature of only some disciplines in ecology and evolution. All ecologists should have a minimum working knowledge of molecular methods in order to recognize where they might be applied. As this shift occurs, we fully expect to see important advances in our understanding of the fundamental patterns and processes that define the field of ecology.

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