

Practice-oriented controversies and borrowed epistemic credibility in current evolutionary biology: phylogeography as a case study

Although there is increasing recognition that theory and practice in science are intimately intertwined, philosophy of science perspectives on scientific controversies have been historically focused on theory rather than practice. As a step in the construction of frameworks for understanding controversies linked to scientific practices, here we introduce the notion of borrowed epistemic credibility (BEC), to describe the situation in which scientists, in order to garner support for their own stances, exploit similarities between tenets in their own field and accepted statements or positions properly developed within other areas of expertise. We illustrate the scope of application of our proposal with the analysis of a heavily methods-grounded, recent controversy in phylogeography, a biological subdiscipline concerned with the study of the historical causes of biogeographical variation through population genetics- and phylogenetics-based computer analyses of diversity in DNA sequences, both within species and between closely related taxa. Toward this end, we briefly summarize the arguments proposed by selected authors representing each side of the controversy: the ‘nested clade analysis’ school versus the ‘statistical phylogeography’ orientation. We claim that whereas both phylogeographic ‘research styles’ borrow epistemic credibility from sources such as formal logic, the familiarity of results from other scientific areas, the authority of prominent scientists, or the presumed superiority of quantitative vs. verbal reasoning, ‘theory’ plays essentially no role as a foundation of the controversy. Besides underscoring the importance of strictly methodological and other non-theoretical aspects of controversies in current evolutionary biology, our analysis suggests a perspective with potential usefulness for the re-examination of more general philosophy of biology issues, such as the nature of historical inference, rationality, justification, and objectivity.

Keywords: DNA-based evolutionary biology, scientific practice, scientific controversy, phylogeography, epistemic credibility, coalescent, population genetic and phylogenetic modeling

1. Introduction

Scientists all over the world are increasingly turning to computer simulations and statistical inferences in their research projects. Therefore, when debates or disputes arise, theoretical considerations are not necessarily central to their resolution. This feature of contemporary scientific research has been noticed by Eric Winsberg, who claims that in computer simulation studies, any underlying theory is just one of many factors involved in interpreting the outcome of simulations and, as a consequence, theory may bear no direct substantive relationship to the

knowledge generated by those simulations (see Winsberg 2006, 2009, 2010). The process of generating scientific inferences using statistical tests may also be removed from theories presumably relevant for the justification of such inferences. This is the case because the generation of results (as well as their interpretation, sometimes) is left in the hands of computerized statistical implementations that are virtually never explicitly designed to deal with the specific situations under study. Moreover, many different statistical approaches (e.g. t-tests, principal components, Bayesian networks, and so on) could be used to address the same questions, but either different individuals or communities of investigators might have contrasting perceptions of the relative merits of those approaches, or of the ways in which they have been instantiated in a computer package.

In fast-developing areas of the life sciences, such as evolutionary biology —with its undeniable geneticized-molecularized ethos— there is plenty of evidence to support the view that researchers are relentlessly interested in the use of ever more ‘powerful’ simulations and other informatic methods, to the point that methods themselves drive entire research lines within the discipline. After years of discussion around ‘the practice turn’ in the philosophy of science, a rising interest from philosophers of biology in methods-related, eminently practical aspects of current evolutionary biology could have been expected. However, several philosophers of biology working in evolutionary matters seemingly continue to follow Ernan McMullin in considering theoretical disputes “the commonest source of controversy in science” (McMullin 1987, p. 66). Studies of controversies at the theoretical level are certainly important, but such metascientific emphasis obscures the fact that several current conflicts in evolutionary biology are linked to the interpretation of results obtained by means of all sorts of modeling tools and similar resources—in short, with the way in which specialists actually measure phenomena, describe processes, and quantitatively address their explanations.

In the present work, we analyze a recent, heated controversy that has taken place inside a high-profile subdiscipline of evolutionary biology called phylogeography. This field, which has been described by two specialists in the subject as a “bridge linking the study of micro- and macroevolutionary processes”, that has “deep roots in historical biogeography and population genetics” (Bermingham and Moritz 1998, p. 367; see also Avise 1998, 2000, 2009 and Hickerson et al. 2010), currently provides an outstanding example of a biological research area heavily driven by methodologies, in most cases implemented in computer programs with ever-increasing degrees of sophistication. Phylogeography provides an ideal case study of an evolutionary biology controversy where theory has been marginal, whereas practice has been centrally involved, in the specifics of the conflict. Although the theory/practice divide is a major guide to our philosophical analysis, we are also concerned with addressing the role that epistemic virtues and/or values (sensu Nola and Sankey 2007) might have been playing in ‘the phylogeography controversy’. Through a joint consideration of these two analytical contexts, we have developed the notion of borrowed epistemic credibility (BEC) to describe the situation in which, to succeed in defeating an opponent in a controversy over methods, a given researcher (a) justifies her stance through an appeal to the set of values that correspond to proper scientific standards in her field, by (b)

invoking similarities in her research practice to practices and values previously established in foreign fields. We claim that our notion of BEC, as developed out of our analysis of the controversy taking place in phylogeography, could be useful to understand how other (biological) scientific controversies that spring from disagreements about methodological issues potentially involve deeper debates about what constitutes acceptable scientific practice, or even over what constitutes 'good science' in general.

2. Phylogeographic theory: a minimal primer

Phylogeography was born in the late 1980s as an attempt to unify the fields of phylogenetics and population genetics, in an explicitly biogeographical context. The international evolutionary biology community universally accepts that the discipline was officially started with the publication of a 1987 paper by American geneticist and evolutionary biologist John C. Avise and collaborators (Avise 2000, 2009; Bermingham and Moritz 1998; Hickerson et al., 2010; Riddle 2008). In that seminal publication, Avise et al. (1987, p. 516-517) stated that "... (a) phylogenetic interrelationships among [segments of DNA] and (b) geographic distributions of the phylogenetic groupings... constitute concerns of a discipline that might be termed intraspecific phylogeography". (Intraspecific) phylogeography rested initially on the phylogenetics-inspired analysis of DNA data from a single genomic compartment: the maternally inherited mitochondrial DNA (mtDNA). However, as the field progressed, nucleotidic sequences from other organelle genomes were successfully tested —e.g. single copy nuclear DNA (scnDNA) from many non-animal species groups, as well as plant chloroplast DNA (cpDNA) exclusively from plants and other photosynthetic taxa (Avise 2009). Likewise, in time the use of the term 'phylogeography' has experienced modifications; for instance, the adjective 'intraspecific' has been substituted by 'comparative' reflecting the historical biogeographers' realization of the conceptual commonalities that Avise's proposal had with biogeography-specific long-term concerns (e.g. Arbogast and Kenagy 2001).

2.1. Population genetics, phylogenetics, biogeography, and the basic goals of phylogeography

According to its original definition, phylogeographic studies take 'phylogenetic thinking' —i.e. graph-like representations of the evolutionary relationships between species, universally associated to the term 'phylogeny' or 'phylogenetics'— and apply them to populations within species —that is, to a 'population genetics' context. With or without the addition of the qualifier 'comparative', the 'geography' suffix in 'phylogeography' alludes to the role of the analysis of the spatial, or (bio)geographical, distribution of genetic variation (Avise 1998, 2000, 2009). As stated above, empirical (comparative) phylogeographic studies are intrinsically molecular —our review of the literature leads us to suggest that DNA-related information is phylogeography's *sine qua non* as a biological research area. Therefore, the first step in any phylogeographic study is the assembly of DNA sequence data from as many individuals and from as many populations as possible from the species of interest. These data are then analyzed with a variety of informatically implemented algorithms to sort the samples into groups. Expectedly, those algorithms embody a number of

different similarity criteria (Avice 2009, Posada and Crandall 2001; Woolley et al. 2008); as we explain later, such divergences at the methodological level are crucial to define the grounds in which the phylogeographic controversy we analyze here has taken place.

Once a hypothesis of the relationships between the populations of a species has been reconstructed, it is then possible to assess the distribution of genetic variation with respect to geographical location. For example, Avice (1992) described a phylogeographic investigation in which this interrelationship between population genetics, phylogenetics and biogeography was clearly exemplified. In that study, a suite of coastal animals including horseshoe crabs, oysters, sparrows, sea bass, and a species of coastal turtle, all with ranges spanning both the Atlantic coast as well as the United States portion of the Gulf of Mexico, showed strong divergence in genetic variants between the Gulf and the Atlantic. Avice found that, in all of these species, the populations in the Gulf shared more similarities with the other Gulf populations than with those in the Atlantic and viceversa. The associations between (bio)geography and (population and phylo)genetics were used to make causal inferences regarding the relative role of 'recurrent processes', such as continual genetic interchange, as opposed to 'unique events' such as the rising of a mountain range (Fig. 1).

In 1998, Avice a paper to celebrate the 10th anniversary of the paper that started the field. In that paper Avice had already counted "more than 130 papers (which) had employed 'phylogeography' in the title or as an index word", adding that "they represent only the tip of the iceberg because numerous additional studies have dealt with the topic implicitly although not by name" (Avice 1998: 371). From her position as one of the main proponents of the 'quantitative model-oriented' school of phylogeography involved in the debate, phylogeographer Lacey L. Knowles recently stated that "the unwavering popularity of phylogeography is indisputable" (Knowles 2009, p. 595) and estimated that 4370 papers where the word 'phylogeography' was explicitly used had been published up to the year 2008. Leaving aside the details of the bibliometric assessments and their support to each side of the controversy over phylogeographic methods (e.g. Knowles 2008), nobody questions that phylogeographic studies have covered all taxa across the 'tree of life' —or, to quote a rather conventional way to express the idea, that they span the entire spectrum between "human migration and the origin of viral pandemics" (Bloomquist et al. 2010).

Fig. 1. Phylogeography examines the geographical distribution of genetic variation within species.

2.2. A common theoretical framework for phylogeography: the coalescent

If compared, the goal of any two or more phylogeographic studies is similar —"to understand the processes underlying the spatial and temporal dimensions of genetic variation" (Knowles 2009, p. 593; notice again the emphasis on genetic diversity, not on the organisms carrying it). A key theoretical element of phylogeography that is common to all (competing) perspectives in phylogeography has been generally referred to as the coalescent. The theory of coalescence was

presented as an independent mathematical elaboration closely connected with the theoretical framework of population genetics by Kingman (1982), Hudson (1983), and Tajima (1983), with the aim of providing a formal framework to trace present day genetic lineages back in time to their most recent common ancestors. According to this theory, (genetic) coalescence is the reverse of (genetic) divergence: as we move forward in time, we can think of an individual DNA molecule replicating and siring two new (genetic) lineages; such events are the so-called divergences. Looking backward in time, whenever two (genetic) lineages merge into the same ancestor, researchers say that they 'coalesce'.

Coalescent theory translates the intuitive notion stated above into a series of idealized mathematical models whose main goal is to calculate the time elapsed between the most recent common ancestor and the genetic variants found in present day populations. Given the highly idealized nature of the models, researchers modify some of the premises of the coalescent model to approximate results from real-life populations; for example, coalescent times are expected to be much longer for genetic loci that recombine than for those that do not (McVean and Cardin 2005). Basic versions of the coalescent, though, assume that all members of a population are equally fit, a condition never observed in nature. In response, variation in factors such as survivorship or fecundity is included in the model (O'Fallon et.al. 2010). By the same token, levels of genetic diversity can be taken into account in calculating population size, wherein a small population with high genetic diversity could be considered as representing more individuals in a genetic sense than a very large but genetically uniform population (Nei and Takahata 1993). Similarly, different mutation rates will also be associated with different coalescence times, *ceteris paribus*. All of these modifications are introduced to make the models as close to the actual world as possible, but as models become more realistic, the resulting algorithms become less tractable as the number of possible evolutionary scenarios that can be depicted increases enormously with each new variable. It is in this context that methods that apply the coalescent to phylogeography proliferate, as each emphasizes different combinations of realism, generality, and inferential power.

2.3. Coalescent theory in two different methodological contexts: nested clade phylogeographic analysis (NCPA) versus the approximate Bayesian computation (ABC) approach

Nested clade phylogeographic analysis (NCPA) is a phylogeographic method developed by American evolutionary geneticist Alan R. Templeton (Templeton 1987, 1998, 2001, 2002, 2006, 2008, 2010a; Templeton et al. 1995; Castelleo and Templeton 1994). Templeton's NCPA (originally named NCA; Templeton et al. 1995) has been widely considered to be the most popular phylogeographic method, particularly by some of its detractors (e.g. Petit 2008a, 2008b). In brief, NCPA operates by estimating the genealogical relationships between DNA segments sequenced from samples obtained from throughout the range of a given species. The branching diagrams resulting from the computerized NCPA analyses are known as 'haplotype networks' (Fig. 2)¹. The 'nested clade' aspect of NCPA —where the semantics of clade are only partially equivalent to the meaning of that word in cladistics and other research programs in phylogenetics— refers to a step in which the haplotypes are arranged into a nested hierarchy of groups that are separated by one

or more mutations. The corresponding computerized algorithm then calculates by null-hypothesis testing a pair of indices that reflect expectations regarding how widely haplotypes are distributed, how abundant they are, and how far they have moved historically. Significantly large or small indices are taken as indicating processes such as geographical range expansion or shifts in the center of distribution. To interpret the indices, Templeton et al. (1995) provided an inference key that constituted the initial basis for all NC(P)A studies. The inferences drawn with the key were supposed to be deductive consequences of what should obtain, given the general expectations of coalescent theory. Accordingly, different evolutionary scenarios —e.g. random mating, gene flow with isolation by distance, sudden range expansion, long-distance dispersal, or events that divide one large population in two smaller ones— should produce differing patterns of significance of the main indices calculated with the associated software (see Templeton 2009a, 2009b).

3. The ‘phylogeography controversy’: not about theory, but about practice

Templeton’s proposal of NCPA as an analytical tool in phylogeography was not initially meant to form the basis of a ‘phylogeographic school of thought’, analogous to the methodological stances involved in the ‘phylogenetics wars’ of previous times (for a classical and two recent but contrasting accounts of those disputes, see Hull 1988, Felsenstein 2005, Williams and Ebach 2007). The actual conflict between the NCPA phylogeographic viewpoint and an alternative perspective only became clear in 2002, when Knowles and evolutionary biologist Wayne P. Maddison published a criticism of what they saw as “primarily non-statistical” methods to reconstruct phylogeographic history, through which “inferences about particular biological processes (are made) without explicit reference to stochastically derived expectations” (Knowles and Maddison 2002, p. 2623). In their article, Knowles and Maddison also advanced the view that “phylogeographic methods that make both explicit statistical links between process, prediction and test (like the coalescent-based population genetic models) and consider a diverse array of processes of histories (like NCA)” (Knowles and Maddison 2002, p. 2624). The latter mention of NC(P)A is, however, not used by these authors to establish a commonality of interests as their main objective, but to differentiate their approach from Templeton’s program. In the same page, Knowles and Maddison choose the “statistical phylogeography” to identify their stance, a name that has been preserved in many subsequent publications that represent what might currently be the strongest side in the controversy (see Knowles 2004, 2008, 2009, Nielsen and Beaumont 2009, and Panchal and Beaumont 2010, among others).

Using a similar strategy of criticism, other statistical phylogeographers have later made the additional charge that phylogeographic inferences are best performed through the use of a family of Bayesian-based statistical models, the most popular of which is called approximate Bayesian computation (ABC; see, for instance, Nielsen and Beaumont 2009). To test phylogeographic hypotheses with an ABC model, the statistically-oriented researcher proposes a small set of hypotheses that might account for the geographical distribution of genetic variation observed at

present. Given the data set, which consists of DNA sequences, the evolution of the set of samples is modeled back in time. Different values for variables such as population size and subdivision, number of generations, mutation and migration rates, and other factors of interest, are built into the model. These factors influence the rate of sorting processes, and thus how likely two haplotypes are to coalesce into one. Because sorting processes are stochastic, statistical phylogeographers state that the exact topologies of the genealogies in each round of modeling will often differ. By repeating the model many times, they claim that it is possible to see how often results support or contradict a given hypothesis (for a more detailed discussion on Bayesian methods see Beaumont et.al. 2010; Nielsen and Beaumont 2009; Beaumont and Rannala 2004; or Huelsenbeck 2001).

It is crucial to note that neither the 'inference key', non-statistical model-based' nor the 'model and statistics-based' sides in the phylogeography controversy have declared that genetic lineage divergence/coalescence should not be modeled. Throughout his numerous defenses of his own method, Templeton has in fact admitted that both approaches could be used under certain circumstances (see Templeton 2009a, in particular). Despite this recognition, criticism of Templeton's stance by the NCPA detractors has been forcefully directed at its presumed 'non-statistical' nature. According to Knowles and Maddison (2002) and Knowles (2004, 2009), NCPA analyses based on datasets made up of just one small region of DNA rather than several, ignore the randomness associated with the coalescent process and the accumulation of mutations. The concern of these 'statistical phylogeographers' is then unrelated to coalescent theory per se, but instead with the statistical error in the inference. Knowles and Maddison (2002) asked: "Does NC[P]A then fill the role desired of a flexible, statistical inference procedure?" (p. 2631), answering that NCPA "does not attempt to distinguish statistically among alternative interpretations, nor does it provide an estimate of the uncertainty in its conclusions." They additionally contended that "for any interpretation derived from Templeton's inference key, we cannot ascertain the confidence limits on the reconstructed history, whether they are so broad as to include many unconsidered alternatives, or if an alternative hypothesis would be almost equally well supported by the data" (p. 2624).

Similarly, in a recent critique of NCPA, Panchal and Beaumont (2010) took issue with its statistical aspects, but their mention of any underlying phylogeographic theory was secondary. Regarding the coalescent, Panchal and Beaumont (2010) only stated that the theory for dating clades in NCPA is based on the standard coalescent, but is then applied to scenarios that explicitly do not correspond to it. Rather than finding errors in the way that NCPA flows from coalescent theory, Panchal and Beaumont (2010) followed Knowles and Maddison (2002) in asserting that the method suffers from high false-positive rates; explicit mention of theory in criticisms of NCPA only appears in Beaumont et al. (2010). Panchal and Beaumont (2010) also criticized that the method's testing approach cannot distinguish between scenarios such as restricted gene flow caused by isolation by distance, or those caused by long-distance dispersal. Templeton's preoccupations have been also fully and almost exclusively concerned with methodology. In a recent letter, he

said that his “main objection to ABC was that it can produce posterior ‘probabilities’ that are not true probabilities” (Templeton 2010b, p. 488), and that “the potential of ABC is currently not realized because of serious statistical and mathematical flaws” (p. 489).

Given that the two groups in conflict do not seemingly have any real differences in their understanding or support of the coalescent as a valid model, we consider that the theoretical level plays no major role in the phylogeography controversy. Furthermore, we claim that the core of the controversy lies in the choice of sources of epistemic credibility that have been used to defend either the NCPA or ABC approaches. To defend this claim —namely, that the phylogeography debate is centered on the different sources of epistemic credibility—we further develop our philosophical framework, and then revisit the controversy.

4. ‘Borrowed epistemic credibility’ and the phylogeography controversy

The basic notion behind the conception of epistemic credibility (EC), and the derived notion of borrowed epistemic credibility (BEC), comes from our observation of a number of instances in which scientists do not use empirical arguments to justify their theories, methodologies, or even their results, and consequently appeal to other, non-empirical elements. In our case study, scientists appeal to a large set of elements that include factors considered important in their field or in similar areas of research. The elements that scientists select from these sets are important because they represent what the members of the field mean by objectivity, rationality, or other considerations that a given community takes as the standards of ‘good scientific practice’. Usually, scientists seek to justify their theories, methodologies, or results by connecting them in some way with these sets of considerations.

For the sake of clarity, we will divide the set of considerations scientists take as representing the standards of ‘good science’ into two sets, called cognitive and social values. Following conventional definitions from the specialized literature (e.g. Longino 1990; Lacey 2005; Kincaid, Wylie and Dupré 2007, Douglas 2009), cognitive values are those traditionally regarded as being constitutive to science and include, for example, simplicity, or predictive and unificatory power. On the other hand, social values traditionally have been regarded as not being constitutive to science —for example, norms, beliefs, or moral preferences. However, the aforementioned references also discuss the idea of value-free science (i.e. Longino 1990; Kincaid, Wylie and Dupré 2007, Douglas 2009) showing that there is close interaction between these two subsets, and that therefore it might not be entirely correct to say that social values are not constitutive to science. In any case, for the purposes of our paper we will draw the line saying that cognitive values are a direct function of empirical data. For example, labeling something as ‘simple’ amounts to saying not only that it involves a few variables, but also that these variables interact in linear ways or that they are highly correlated. On the other hand, social values work at a different level with respect to empirical evidence in that data are not judged on their own but according to some previous notion. For example, taking one statistical method to be better than others for data evaluation has nothing to do with the results at hand but with some previous belief.

Having distinguished between cognitive and social values, it is important to remember that they are subsets of those considerations that groups of scientists regard as good science. Scientists wish their claims to conform to what they (i.e. their community) consider as good science. Ideally, scientists should be able to defend the merits of their claims on the strength of empirical evidence alone, but there are cases in which experimentation does not provide conclusive evidence to support such claims. In these cases, support can come from the social values subset (for similar claims see Rudner 1953, Longino 1990, Chang 2004, and in a critical tone Douglas 2009). If empirical evidence alone cannot provide conclusive elements to support a given claim, then the claim needs to be supported further by a series of social values. We suggest that, when confronted with an opponent in a dispute, scientists seek credibility of epistemic nature as a strategy to support their claims and defeat those opponents. Borrowing epistemic credibility (BEC) therefore *means constructing an argument in which a researcher connects her claims to the subset of social values, by invoking a similarity of her research with previously accepted claims that have a well-established set of values*. A key point of our analytical proposal is that, when scientists borrow epistemic credibility, there is an implicit rhetorical element to their attitude: to say that, if the defended claim resembles in any sense the methodologies, theories, models, or results produced in separate fields, then it should somehow also possess their values, is a rhetorical move. According to our analysis, when scientists have successfully borrowed epistemic credibility for their defended claims, they have also been effectively endowed those claims with values that in turn constitute their (only substantial) justification.

4.1. How, and from where, is epistemic credibility borrowed? The general case

Epistemic credibility can be borrowed in different ways, and from diverse sources. To illustrate the process, we suggest introducing a simple abstraction, which is useful to re-address our case study (or other case studies). In this abstraction, A might represent some prestigious scientific research coming from an origin field (OF), and B might stand for work in search of credibility, carried out in a target field (TF; clearly, for our study case, this target field is phylogeography as a biological research area). If there is similarity between A and B, then borrowing epistemic credibility amounts to stating that B also exhibits A's values, which in turn justifies that members of the community in TF accept B. Note that the burden of proof for B lies entirely on an argument for analogy between the situation in OF vis-à-vis its equivalent in TF. With this simple formalism in place, it is possible to describe the different sources of epistemic credibility.

Robustness of method can be considered a source of epistemic credibility (EC). B borrows robustness of method-related EC by virtue of its results being the same or analogous to those obtained in A. Another source of EC could be bootstrapping, in which the results in B are not the same, but resemble the kind of results generated by A. Appeal to (established rules of) logical inference may also be considered a source of EC, when B's claims are justified because they conform to a notion of logical inference represented (in OF) by A. In a similar way, quantification might be regarded as another class of EC, when claims based on quantitative results in A are presented as superior to qualitative ones obtained elsewhere. Finally, EC may also be obtained from sources such as tradition or appeals to the authority of prominent scientists whereby the

results obtained using a certain methodology are justified because either an expert, or a group of individuals regarded as experts in their field, sponsor a given methodology (see table 1).

At this point, a critic may wonder how the previous work came to be recognized as representing good science. Would it be the case that our BEC framework entails an ‘infinite regress problem’?² At least in the case of phylogeography, the answer is negative. As a target field, phylogeography has inherited its structure from the suite of primary disciplines —phylogenetics, population genetics and biogeography— that gave birth to it. Phylogeography has acquired its theoretical background and basic methodologies from those origin fields (i.e. the coalescent, the suite of techniques involved in phylogenetic analysis, and a series of mathematical models articulated around the notion of ‘population’), as well as their cognitive and social values. Now, because the different fields that formed phylogeography cherish different social values, we claim that current controversies in the area are the result of the tension between disparate visions of what phylogeography ought to be. The competing visions can be traced in the different sources of EC and the way phylogeographers use them to advance their positions.

Table 1. Sources of EC borrowed in the phylogeography controversy. This tabulation suggests extension of the BEC framework to other controversies, either within evolutionary biology or elsewhere in the life sciences.

4.2. How, and from where, is epistemic credibility borrowed? The phylogeography controversy as a case study

One of the most popular sources of BEC in phylogeography is what we have called ‘logical inference’, meaning an appeal to what each phylogeographer understands as valid or established, rules of logical inference. For example, both sides seem to agree on Popperian falsificationism as an ideal of scientific inference. NCPA has been defended as a Popperian approach because it successively subjects null hypotheses to rejection (Templeton 2009a). Templeton charges that, if the pool of all plausible hypotheses is considered, then successively rejecting competing hypotheses will lead to a “strong” inference (in the sense of Platt 1964, see also Chamberlin 1897, Beard and Kushmerick 2009). In contrast to NCPA, because ABC models can only compare the relative fits of a small number of modeled scenarios, it cannot be considered strong scientific inference. The conclusion drawn is that NCPA should be preferred because it conforms to the rules of (some sort of) formal logic, e.g. when Templeton mentions that “the statistics or probabilities used to measure the goodness of fit of the models obey the constraints imposed by formal logic” (2010c: 6376).

Supporters of ABC do not refute the view of Popperian falsificationism as a valid approach, and indeed seem to share it with supporters of NCPA. Instead, they accuse NCPA of being inductive, traditionally presented in evolutionary biology as the antithesis to Popper and indeed to science (Mayr 1982), such as when Beaumont and Panchal (2008, p. 2564) say that “Templeton (2008) cites Popper (1959) in support of the NCPA approach against model-based statistical analysis. However, we would suggest that although NCPA consists of a large number of hypothesis tests based on permutation methods, in the end it follows an inductivist paradigm of trying to derive a

general explanation directly from the data... By contrast to NCPA, in model-based analysis [such as the ABC approach], one model is pitted against another in the face of the data, and this, surely, is a more valid scientific approach" (Beaumont and Panchal 2008, p.2564).

A large part of the NCPA controversy seems to deal with which is the most appropriate way to analyze phylogeographic data (Bloomquist 2010). Put differently, this controversy deals with which method best represents what the community regards as a good scientific inference. Templeton and collaborators borrow credibility in support of their claims from the long tradition in phylogenetics that has endorsed Popperianism. In doing so, what Templeton is saying is that NCPA should be preferred because it represents an example of what other phylogeneticists have considered as scientific inference. Likewise, Beaumont, Panchal and ABC defenders in general, borrow credibility from the recent surge of Bayesianism in evolutionary studies to back their assertions (for a review see for example, Huelsenbeck 2001).

Another source of disagreement is over the value of verbal versus quantitative reasoning. For example, Beaumont and Panchal (2008) charged that "A verbal, reasoned, argument is presented in Templeton et al. (1995) to justify the method, and the inferences it makes, not dissimilar in style and authority to the *Corpus Aristotelicum*. The authors of 265 papers that have used NCPA are, in a sense, appealing to this authority. One needs to ask: is this science?" (p. 2564). The appeal to what counts as good science is explicit in Beaumont and Panchal's critique of NCPA. In the view of these authors, at issue is not the argument presented by Templeton and colleagues, but the value of verbal reasoning.

Other instances in which phylogeographers search for epistemic credibility involve notions of robustness –the retrieval of known results through the use of different approaches, as well as familiarity, which refers to approaches that produce results congruent with prevailing views. Familiarity and robustness have long been held as standards of good science. For example, Newton-Smith listed them among his standards of "good scientific theories". He said that a good theory should preserve the observational success of its predecessors, and that theories should have a good track record (Newton-Smith 1981: 226-232). Templeton does not shy away from these long-held values to support NCPA and attack ABC. Examples can be found in Templeton's critique of Fagundes's use of the ABC approach to contrast three different models of human evolution (Templeton 2008, 2009a, 2010). Templeton charges that one of Fagundes's models is contrary to the prevailing notion of isolation by distance between humans living in Eurasia and Africa, noting that "it is patent that the parameter values chosen by Fagundes et al. (2007) are strongly discrepant with the empirical data on autosomal coalescent times" (Templeton 2009a, p. 323). Templeton invokes robustness and familiarity of the results, alluding to other controversies in evolutionary biology to show that ABC models do not reach the conclusions generated in similar fields.

As a final instance, epistemic credibility is frequently borrowed from different representations of authority. A conspicuous example is Beaumont et al. (2010), in which 22 authors unite in a single paper to express their reserves regarding NCPA and their support of ABC models. The message of

this surfeit of authors would seem to be that the endorsements of many scientists against one approach implies that it is incorrect. A similar implication that solitariness is associated with the incorrect position is when Beaumont and Panchal (2008, p. 2563) note that “there is a disagreement between Templeton (2004, 2008), who suggests the method works well, and three independent groups (Knowles & Maddison 2002; Petit & Grivet 2002; Panchal & Beaumont 2007), who believe that they have demonstrated that it does not. As far as we are aware, there are currently no publications other than those of Templeton and co-workers to support the accuracy or efficacy of NCPA.”

The preceding instances represent the appeal to the authority implied by consensus among many scientists, but another source of EC can be to appeal to the authority of a single prominent figure. Knowles (2008, p. 2712) exemplifies this when she refers to authors who voice “other concerns over the validity of NCPA’s inferences.” Among these authors she cites American evolutionary geneticist and bioinformatician Joseph Felsenstein, one of the leading developers of the methods used for reconstructing the evolutionary relationships of organisms (see, for example, Felsenstein 1985, 2004, or 2008). Given his prominence in phylogenetics, his verdict against NCPA would naturally have considerable weight. However, the only reference to NCPA in Felsenstein’s well-known treatise on phylogenetic inference (Felsenstein 2004) has the following structure: “A more statistical approach was taken by Templeton (1998), using the nested clade analysis tree reconstruction methods introduced earlier by Templeton et al. (1988). Although well-defined enough to be implemented by computer programs (Clement, Posada, Crandall, 2000; Posada, Crandall, and Templeton, 2000), these methods do not attempt to take into account the uncertainty of the estimate of the tree, and there has been little study of their statistical properties. A notable exception is the paper by Knowles and Maddison (2002). Although the need to use manual steps in the analysis limited the number of replications they could make, they found that the single-tree approach was problematic.” (Felsenstein 2004, p. 484).

In contrast to the assertion of Knowles (2008), Felsenstein does not express anything that can be construed as ‘other concerns’ beyond what had already been discussed in the literature. As a result, we can only interpret Knowles’s citation of Felsenstein as an attempt to borrow credibility from his authority, to shore up her position. Finally, Rémy Petit (2008a, p. 1404) appeals also to authority —of institutions, in this case— when he concludes that “the results of Panchal & Beaumont (2007) convince me that reputable journals should (i) discourage the use of the NCPA method for single locus data sets (...), and (ii) still be suspicious of NCPA analyses based on multiple loci”. Reading between the lines of Petit’s argument, any journal publishing NCPA studies should be held in suspicion.

5. Epistemic credibility, the phylogeography controversy, and the theory-practice divide

Thinking of theory as standing separately from practice has a long tradition in the philosophy of science. As a result, philosophers of science have an extensive battery of conceptual tools at their disposal to think about the theory-practice relation. The vocabulary of laws and axioms, of the

distinction between models and theories, syntactic and semantic relations to the world, as well as notions of theories as explanatory devices all stem from the conception of theory as being in some way distinct from practice. The view of theory as interacting inextricably with practice has less of a tradition, and because of the complexity of this view, much conceptual machinery remains to be built (see for example Burian 2005, Martínez, 2003, Keller 2002, Rheinberger 1997, Pickering 1995). Here, we have offered the notion of borrowed epistemic credibility (BEC), which we believe can contribute to a better understanding of how theory and practice interact to construct scientific knowledge.

We do not claim that scientific controversies closely linked to practice and/or methodology exclusively rest on epistemic credibility. However, we argue that epistemic credibility is likely to play an important role in controversies in which empirical results alone cannot help settle the differences. For example, scientists involved in the molecular clock controversy indirectly appealed to epistemic credibility (Dietrich and Skipper 2007). We find a similar analytical context in Winsberg (2006, p. 2), who states that the credibility of a simulation model comes not only from its governing theory, but also “from the antecedently established credentials of the model building techniques employed by the simulationists”. In these examples, and similar to what we have seen in phylogeography, scientists have had to look for arguments beyond theory and its empirical consequences to settle a theoretical dispute or to justify particular modeling practices. However, whereas Dietrich and Skipper and Winsberg make reference to extra-theoretical elements in the context of epistemic virtues and/or the social aspects of science surrounding scientific disputes, our framework places BEC at the core of scientific controversies, not at the periphery.

Our framework also highlights how two traditions within evolutionary biology are the sources of BEC for phylogeography. For example, theory in the form of the coalescent may play no role in the controversy but Popperian falsificationism is often cited. This is not a particular love affair phylogeographers have with Popperianism, but is instead a long-lasting relation that prominent research groups within systematics and evolutionary biology have had with Popper’s vision of science since the 1960s. As discussed by Rieppel (2008; see also Stamos 1996; Helfenbein and DeSalle 2005), the falsification of hypotheses has been perceived as a crucial component of ‘good scientific practice’ for decades by a large number of systematists and evolutionary biologists. Templeton’s borrowing of epistemic credibility from Popper follows in the footsteps of this tradition; its weight also explains why not even ABC supporters challenge the Popperian ideal, but instead try to show how NCPA is not really an example of falsificationism.

In a similar way, one can trace back sources of epistemic credibility in the debate to other important values held by different schools within evolutionary biology. To name some examples, different schools defend their own interpretations of statistical inference (see Sarkar 1992), the value of graphical versus mathematical representation (see Petit 2008), or the value of graphical versus mathematical reasoning (Beaumont et.al. 2010). Perhaps this example of an intellectual tradition within a guild of scientists illustrates the social dimension of knowledge. From this point of view, normativity is a rational standard provided by a community (see for example Hacking 1992 or Kusch 2002). Applied to our case, phylogeographers in disagreement represent two

communities within evolutionary biology that have quarreled for decades over the correct way to conceptualize their field, evolutionary history, and science itself. Each community defends a particular set of values that in a sense reflect a style of reasoning that as Hacking argues, becomes “a timeless canon of objectivity, a standard or model of what it is to be reasonable about this or that type of subject matter” (Hacking 1992: 10). The values defended by each community are made explicit in the sources from which epistemic credibility is borrowed by NCPA and ABC supporters. If this is correct, then it should be possible to reconstruct the intellectual history of evolutionary biology to show how and why (at least) two parties emerged and what their differences are. Perhaps such analysis could help find ways to work out the differences.

Our study also highlights other pertinent questions of the theory-as-practice view. For example, science evolves via a continual anastomosis of practices and concepts. Phylogeography is an excellent field to address such view, because it is a synthetic discipline forged by the union of phylogenetics, biogeography, and population genetics (Avice 2000, Avice 2009, Hickerson et al. 2010). If phylogeography is a good instance of a synthetic field at all, then it would seem that these fields do not emerge out of the construction of novel theory but from the pulling together in the laboratory of disparate research traditions. Theory, along with practice generally construed, and the set of values used to justify certain claims, may be inherited from the different fields being brought together, but it is by no means clear why certain elements make the step to the new field, or how theory originated within the new field is constructed. However, the conceptual tools that we propose here can illuminate some aspects of the forging of synthetic disciplines by exposing the web of distinct elements imported from other fields and how they are used to construct a new discipline. Again, the notion of epistemic credibility is vital as the new discipline imports not only theory and methodologies but, as the phylogeographic debate illustrates, what the members of the new community should take for rational, objective, valid or scientific.

The search for epistemic credibility, and its borrowing from areas of knowledge that in principle lie far from the theories and practices that are traditionally claimed as properly biological, is not restricted to phylogeography. The clearest examples come from disciplines in which the merits of theories or practices in general cannot be evaluated by experimentation, for example, areas in which the experiments needed to resolve a controversy conclusively would be so difficult to carry out and interpret that scientists must appeal to other sources to defend the empirical data. So, while the borrowing of epistemic credibility is particularly well illustrated by phylogeography, there is good reason to suspect that it characterizes controversies throughout biology where claims cannot be supported by empirical evidence alone. Even more importantly, it provides a tool for describing the ways in which controversies in science take place at a remove from theory.

Figure 3. Diagrammatic representation of the set of controversies in phylogeography. **Phylogeography is a synthetic discipline formed from the union of different disciplines within evolutionary biology. The controversies are represented, first, as a controversy between model-based and non-model based methodologies (central circle). Second, as a controversy about phylogeography itself as competing groups appeal to different sources of BEC based on**

particular notions of what counts as good science (outer circles), and finally, as a controversy about science itself.

6. Conclusion

The polemics surrounding NCPA illustrate how a seemingly methodological controversy is in effect a larger debate confronting two visions of what science should be. This larger debate is evident in the numerous sources of epistemic credibility borrowed by the participants and the scant presence of coalescent theory. From a philosophical perspective, we illustrate a case of scientific controversy that takes place largely in the realm of practices. In our analysis, the interplay of theory and practice-based controversies, scientific evaluation using social values, and the web of conceptual relationships traced by the borrowing of epistemic credibility, contrasts with the traditional conception of theory as separate from practice. Instead, our analysis adds support to the increasing recognition of the inseparable reciprocity between concepts and practice in science.

Our analysis also highlights an important social component to the practice of science and the generation of knowledge. The sources of epistemic credibility invoked in this particular controversy are not simply rhetorical devices used to defend a particular methodology, but trace the evolution of the field of genealogical studies by exposing the epistemic, methodological, and theoretical commitments shared by its different communities. Our reconstruction shows how the controversy transcends the particulars of ABC versus NCPA to deal with numerous fundamental disagreements in terms of the importance of gene trees, the need to automate the inference process, the importance of formal inferences, and in general the sources of epistemic credibility that justify the claims of a given community. Perhaps, then, this controversy is another chapter in a long debate evolutionary biologists have had to understand better their field, and science in general, and shows how complex practices, in which the distinction between theory and practice is difficult to demarcate, begs revision of notions of the nature of explanation and how scientists define the appropriate structure of inferences.

Footnotes

1 'Haplotype' denotes any particular DNA variant. The DNA segments used in these studies have numerous positions, each of which may have different states across the individuals sampled. These states can be manifested as substitutions of different bases (G, A, T, or C), or by the presence or absence of a base at a given site (known as an indel, or insertion-deletion event). Different individuals have different combinations of substitutions and indels. Each unique

combination of states characterizing a sequenced segment of a DNA molecule is referred to as an haplotype.

2 Talk of prestigious works or individuals begs the question of how can we evaluate such thing as prestige. However, it is clear that the academic world has constructed operational indicators (citations in prestigious journals, awards received or funding, among others) that empower some groups and individuals. We believe that communication between members of particular research communities help transmit information on the identity of those groups and individuals (see, for example, Bollen et al. 2006, Cronin 1999, Franceschet 2010, Wegener 1992, and Newman 2001).

7. References

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