### 論文題目

## Pattern and Process of Language Evolution in the Japanese Islands

(日本列島における言語進化のパターンとプロセス)

氏名

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### **Chapter One**

### Introduction

All life on Earth is the product of evolution. From simple molecules to exquisite animals, life existed on Earth for some three thousand millions years, without ever knowing the awesome machinery of natural laws that constantly changed the way they were. Then the truth finally dawned on one of them, whose name was Charles Darwin. After Darwin's discovery of the elegant truth that all living organisms, including us, evolve by descent with modification, our understanding of nature and our place within it was never the same again. Evolution is a fact, but its implications are yet to be fully realized as we are still making astonishing and unexpected discoveries about its deep relationships not only with ourselves but also with an essential constituent of our species' way of living, which is our language.

The idea that languages are as much the product of evolution as biological organisms has a long history. It was first conceived by August Schleicher (1869) soon after the publication of the *Origin of Species* (Darwin, 1859), and Charles Darwin himself also alluded to the curious parallels between biological and linguistic evolution in *The Descent of Man* (Darwin, 1871). The beginning of these ideas were humble and speculative in nature, but we now know that they were deep and profound, and modern science would eventually verify their validity (Atkinson & Gray, 2005). Of course, it is too early to say that we have reached a complete understanding of how languages come into being, evolve, and perish. But we know that we are approaching one of the greatest mysteries of human sciences.

In this thesis, I attempt to advance our understanding of how languages evolve through discussing some specific examples that represent two major dimensions of evolution. One dimension is the *pattern* of evolution, which is exemplified by the spectacular diversity of biological and linguistic forms on Earth, and its discernible regularity through the lens of quantitative methods. The other dimension is the *process* of evolution, which is exemplified by the unmistakable natural laws giving rise to the ever-diversifying biological and linguistic forms, and their merciless pruning forces that shape the complex trees representing the history of life and language.

Thus, throughout the following chapters, when I make observations about variation among languages and chart out their evolutionary history in space and time, the matter of concern is the pattern of language evolution, and similarly, when I make observations about the possible causes that might explain the changes in spatiotemporal variation among languages, the matter of concern is the process of language evolution. I suggest that these two dimensions not only provide a suitable framework for organizing scattered pieces of evidence but also two complimentary ways of looking at the same truth: the observed regularity of nature (pattern) provides direct clues about its underlying mechanism (process), and with a good understanding of the mechanism, we can further refine the way in which the regularity is quantified (pattern).

The two dimensions of pattern and process can also be phrased differently, such as What questions and Why questions of biology (Mayr, 1998); Mode and Tempo in macroevolution (Fitch & Ayala, 1994); Functional and Phylogenetic explanations of evolution (Tinbergen, 1963). Each of these phrases suggests that scholars of different fields all recognize the need for studying evolution in some structured ways, but at the same time, the fact that there are various phrases to

represent a similar idea also suggests that precisely how the conceptual framework should be defined is a difficult matter and far from reaching a consensus. Thus, I refrain from claiming that the phenomenon of language evolution can be perfectly contained within a neat verbal phrase such as pattern and process. It should be noted, however, that the concept of pattern and process is a means, not a goal.

Perhaps a major difficulty pertinent to adopting the framework of pattern and process is that we require a set of presuppositions, which may or may not be valid, to ignite the engine of inference. More specifically, in order to study evolution in terms of its pattern and process, we must first begin by quantitatively sketching out the pattern, as we cannot move forward to investigate the process underlying the phenomenon of interest unless we know what it is that we are dealing with; but the quantification of the pattern itself cannot be done without bearing a set of presumptions, or a model, about the process of evolution such as how fast substitutions occur (for nucleotides or cognates) or how much influence selective pressure (as opposed to drift) has on the substitutions (Sober, 1991). Thus, if we start with inappropriate assumptions to make observations of the pattern and then move on to make further elaborated inferences about the process, there is a potential danger that we might end up taking the trajectory of serial false inferences.

In order to avoid being trapped in a loop of fruitless research, I suggest five different but interrelated research protocols, which naturally are deeply embedded in all studies presented in this thesis. First protocol is to never forget that all our process presuppositions are merely a working model that should not be accepted as truth, but used carefully and selectively based on its usefulness (Sterman, 2002) in explaining the past events (Hempel & Oppenheim, 1948) or predicting the future events (Lakatos, 1977). Put differently, I suggest that we

should start with the most plausible assumptions about evolutionary process available at hand, but be aware that our knowledge of process is meagre, so the plausibility of a model must be subjected to iterative verification between empirical testing and explanatory/predictive usefulness. As George E. P. Box remarked, "all models are wrong, but some are useful" (Box & Draper, 1987). We must not hesitate to reject the old presuppositions if more useful ones come along. This is an abstract rule of conduct, but a truly important philosophical standpoint required for continuous scientific progress.

But one might wonder, how much process presupposition is necessary for making the initial inference about the pattern, or put more simply, where the starting point should be. This question brings us to the second research protocol I suggest: we must start with simple assumptions that capture the general algorithm of evolution, and gradually increase the complexity as necessary (Atkinson & Gray, 2006). Elliot Sober (1991) refers to this practice as "less is more", meaning that the less one presupposes about the evolutionary process for making a pattern inference, the more confidence one can have in the conclusion. This is because simpler models have superior testability (Popper, 1992) and are more informative (i.e., having a higher performance/parameter ratio) (Sober, 1975). If there are two different sets of presumptions that are equally useful, then the one with the fewest and simplest presumptions should be the starting point of investigation. It should be noted, however, that just as Occam's razor, this protocol is rather a heuristic for general guidance than an irrefutable principle of logic.

More specifically, as we accumulate more knowledge about how evolution works, more and more complex process assumptions are being recognized as realistic and useful (Felenstein, 2004). For example, modern phylogenetic inferences are dominated by complex stochastic models that assume changes in substitution

rates for certain sites and/or branches of phylogenies, and these models easily outcompete simpler approaches such as maximum parsimony or distance-based methods that lack this assumption (Saitou & Nei, 1987). However, as we increase the complexity of a model with seemingly realistic and useful assumptions, we can run into problematic situations where we end up "fitting an elephant" to the data with rather redundant parameters (Steel, 2005), and this problem can be further magnified by the inevitable statistical tendency that incorporating more parameters almost always leads to improvement of model fit to data. Accordingly, I suggest adopting the third protocol to alleviate the problem: when we have many seemingly realistic and plausible models at hand, we should exhaustively compare all models to one another, and select a model that captures the general algorithm of evolution while maintaining the balance between simplicity and biological realism (Johnson & Omland, 2004; Posada, 2003). Obviously, this is a formidable exercise that requires us to adopt some objective criteria for determining what qualifies as a model that best balances simplicity and realism. Fortunately, there are several useful criteria such as Akaike Information Criterion (AIC) (Akaike, 1973) or Bayesian Information Criterion (BIC) (Schwartz, 1978) that consider the trade-off between the usefulness of a model and its complexity, by penalising the model as a function of increased number of parameters. The more evolutionary models one explores with these criteria, the less one should be concerned with incorporating redundant presumptions.

The fourth research protocol concerns with model uncertainty. The model uncertainty refers to a potential problem of not being able to estimate how plausible the chosen model is, especially when the AIC or BIC is estimated from the outcome of classical frequentist statistics. This is because classical frequentist statistics considers a parameter is unknown but constant, and thus the results can only be represented in point estimates (i.e., the maximum likelihood) with no indication about the model's actual credibility (Omlin & Reichert, 1999). In other words, against our best effort to choose the best model with AIC or BIC, if a model can only produce point estimates, there is no way for us to find out how much uncertainty is involved with the chosen model (Holder & Lewis, 2003; Posada & Buckley, 2004). Preferably, we would be better informed if we have some information about the uncertainty inherent to each model before choosing a particular model over another (Wade, 2000). It would thus be desirable to be able to quantify the degree of uncertainty involved with each model, and it is in this sense that I put forth the fourth protocol: one should, whenever possible, adopt a Bayesian approach to test the plausibility of all candidate models through comparing them directly to one another, and have a good idea about the extent of uncertainty involved with each model; and then choose the best model through, but not limited to, marginal likelihood sampling (Baele et al., 2012; Gelman & Meng, 1998; Newton & Raftery, 1994; Ogata, 1989) followed by evaluating Bayes factors (Jeffreys, 2008; Kass & Raftery, 1995; Sinsheimer, Lake, & Little, 1996). Or, we could even average all uncertainty over many competing models instead of choosing one particular model (Hoeting, Madigan, Raftery, & Volinsky, 1999; Li & Drummond, 2012; Wintle, McCarthy, Volinsky, & Kavanagh, 2003). Using this protocol will enable us to attach credibility to each model and account for the uncertainty inherent in the model selection process.

The final, and perhaps the most effective protocol for avoiding the trap of fruitless research might be to adopt a triangulation method. In other words, we should determine the plausibility of the results derived from the chosen presumptions through cross-verification with other independent evidence such as anthropology, archaeology and linguistics (Gray, Greenhill, & Ross, 2007; Kirch & Green, 2001), and synthesize all historical evidence to check the overall coherence of the chosen model. Just as measuring angles from two known points of a baseline can determine an unknown location of a third point, we can approximate what the outcome should look like by figuring out the converging

point of other independently verified evidence, and by estimating the degree of consistency between the expected and observed outcomes, we can test how good our model is, or whether or not it should be rejected.

W.S. Holt (1933) remarked that studying history is like holding "a damn dim candle over a damn dark abyss". Studying the evolutionary history of languages, or history of anything, is extremely difficult due to a simple natural law that what is gone is gone, and hence cannot be observed directly. Thus, in order to make rigorous inferences about the past, we must rely on informed guesswork, tedious reverse engineering, and never-ending crosschecks. This is a daunting task, but I strongly believe that with sophisticated statistical methods and principled reasoning, it is possible to shed light on the evolutionary history of languages, and see its "ever-branching and beautiful ramifications" (Darwin, 1859).

In Chapter 2, I describe results from a study that attempt to reveal the historical pattern of the Ainu language in space and time (Lee & Hasegawa, 2013). The Ainu language is an endangered language spoken by indigenous people that once thrived in northernmost island of Japan. Despite decades of research, the origins of Ainu people and their language remained notoriously elusive. The prevailing theory, namely the dual-structure model, has long argued that the Ainu are direct descendants of a single ancient lineage from Southeast Asian lineage, and they remained relatively isolated from neighbouring ethnolinguistic groups until present. In stark contrast, recent evidence from several lines of research is beginning to reveal that the Ainu origin seems to be related to a recent population settlement by the Okhotsk people in northern Hokkaido. Based on the premise that population expansions often leave its signature in the patterns of linguistic variation (Cavalli-Sforza, Piazza, Menozzi, & Mountain, 1988; Diamond & Bellwood, 2003), I carried out spatiotemporal analyses on 19 Ainu language fossils, and observed that, in agreement with the recent Okhotsk settlement

scenario, they were estimated to be the descendants of a common ancestor who arose and spread from northern Hokkaido around 1,300 years ago. This finding suggests that the principle factor that shaped linguistic diversity of the Ainu may be the population expansion event by the Okhotsk people, and thus indicate that the prevailing theory of the Ainu being direct descendants of ancient Southeast Asians should be rejected.

In Chapter 3, I describe results from a series of phylogenetic analysis on 59 Japonic languages, and argue that the pattern of linguistic diversity in the Japanese Islands is deeply related with the migration of Yayoi farmers around 2,500 years ago. I also describe several criticisms that have been raised since the publication of these results (Lee & Hasegawa, 2011) and attempt to address them appropriately. Although several scholars raised important and valid issues regarding the study, the arguments I present in this chapter demonstrate that none of the criticisms well founded enough to refute the main conclusion, and I thus maintain the position that prehistoric agricultural population played a crucial role in shaping linguistic diversity of Japonic languages.

In Chapter 4, I describe a potential evolutionary process that could be responsible for much of linguistic diversity of Japonic language family: allopatric language diversification among islands. I measured the degree of linguistic beta diversity with dissimilarity distances, and examined the correlation between the influence of isolation by ocean barriers and the degree of linguistic diversity. Rigorous correlational tests yielded results that were consistent with a hypothesis that good barriers make good languages, and it was also confirmed that the result was not a byproduct of (i) using a distance matrix extracted from an unreliable language tree, (ii) a decay of linguistic similarity as a function of geographical distance, and (iii) accelerated evolutionary rates in languages spoken by small communities. In addition, I compared results from the analysis of variance on

genetic and linguistic structures in the Japanese Islands, and showed that the degrees of pairwise population differentiation between the two structures are highly correlated, even after controlling for geographical proximity. I interpret this finding to imply that the evolution of both systems has been shaped by similar historical factors, and supports the idea that human genes and languages often evolve by a shared process of descent with modification.

Languages are born, live and die. Through internalization of principled research protocols and advanced statistical techniques, this thesis aims to show that patterns of variation among languages preserve the signal of their evolutionary past, and that once a clear picture of the pattern is obtained, it becomes possible to investigate the evolutionary processes that shape the tree representing history of languages. Despite many challenges, I firmly believe that the following chapters demonstrate the way in which we can untangle the complex branches of language trees, and discover the tales of their beautiful ramifications.

### **Chapter Two**

## **Evolution of the Ainu language** in space and time<sup>1</sup>

Languages evolve over space and time. Illuminating the evolutionary history of language is important because it provides us a unique opportunity to shed light on the population history of the speakers. Spatial and temporal aspects of language evolution are particularly crucial for understanding demographic history, as they allow us to identify when and where the languages originated, as well as how they spread across the globe. Here I apply Bayesian phylogeographic methods to reconstruct spatiotemporal evolution of the Ainu language: an endangered language spoken by an indigenous group that once thrived in northern Japan. The conventional dual-structure model has long argued that modern Ainu are direct descendants of a single, Pleistocene human lineage from Southeast Asia, namely the Jomon people. In contrast, recent evidence from archaeological, anthropological and genetic evidence suggest that the Ainu are an outcome of significant genetic and cultural contributions from Siberian hunter-gatherers, the Okhotsk, who migrated into northern Hokkaido around 900 – 1,600 years ago. Estimating from 19 Ainu language fossils preserved five decades ago, I show that they are descendants of a common ancestor who spread from northern Hokkaido around 1,300 years ago. In addition to several lines of other emerging evidence, the phylogeographic analysis presented here strongly supports the hypothesis that recent expansion of the Okhotsk to northern Hokkaido had a profound impact on the origins of the Ainu people and their culture, and hence refutes the dualstructure model.

<sup>&</sup>lt;sup>1</sup> This chapter is based on Lee, S., & Hasegawa, T. (2013). Evolution of the Ainu language in space and time. *PLOS ONE*, 8(4), e62243. doi:10.1371/journal.pone.0062243.s005.

#### 2.1. Introduction

Patterns of linguistic variation among individuals carry the signature of a speech community's demographic past. Accumulating evidence indicates that languages evolve by a process of descent with modification and they form into distinct families in a manner similar to their speakers forming into different ethnic groups through evolutionary history (Cavalli-Sforza et al., 1988; Pagel, 2009). The intertwined history between languages and their speakers appears most vividly in the areas that experienced large-scale population expansions, often driven by agricultural intensification and cultural innovation since the end of the last Ice Age (Bellwood, 2005; Diamond & Bellwood, 2003). Recent empirical evidence supporting this phenomenon stem from a range of language phylogenies reconstructed with computational methods (Gray & Atkinson, 2003; Gray, Drummond, & Greenhill, 2009; Holden, 2002; Lee & Hasegawa, 2011).

While the computational phylogenetic methods have been fruitful in shedding new light on language evolution and the speakers' prehistory, their application has been limited to inferring temporal and sequential aspects. As a result, inferences about the homeland or geographic diffusion pattern often relied on heuristic approaches such as locating a monophyletic outgroup and formulating post-hoc diffusion scenarios from the branching order. Recent progress in phylogenetic methods is, however, producing innovative ways to directly embed phylogenetic inference in a geographical context, and allow us to explicitly estimate both temporal and spatial aspects of evolution while accounting for phylogenetic uncertainty (Bouckaert et al., 2012; Lemey, Rambaut, Welch, & Suchard, 2010; Walker & Ribeiro, 2011). In this study, I adopt these methodological innovations and reconstruct spatiotemporal evolution of the Ainu language: a nearly extinct language spoken by indigenous people of Japan whose origins remain obscure until today. Considerable debate surrounds the apparent incompatibility between the conventional model of human prehistory for the Japanese islands and the emerging evidence from modern archaeology, anthropology and genetics. For several decades, the dual-structure model (Hanihara, 1991) has posited that similarities in dental (Turner, 1990) and cranial features (Dodo & Kawakubo, 2002) between the Ainu people and Southeast Asians meant that the Ainu ancestry originated in Southeast Asia around 10,700 years before present (BP) (Turner, 1986). Similarly, reconstructed proto-Ainu lexicons have also been suggested to share some similarities with proto-Austroasiatic lexicons (Vovin, 1993). Therefore, the Ainu have long been thought to be direct descendants of a single ancient Southeast Asian lineage, the Jomon, and have remained isolated from neighbouring populations throughout the Holocene. However, recent evidence from genetic (Sato et al., 2007; 2009), morphological (Hanihara, 2010; Ishida, Hanihara, Kondo, & Fukumine, 2009), and cultural studies (Masuda, Amano, & Ono, 2001) are beginning to reveal that the Okhotsk people, a huntergatherer group from the Amur river basin, migrated into northern Hokkaido around 900 - 1,600 BP, bringing significant genetic and cultural contributions to the preexisting Jomon, and subsequently gave rise to modern Ainu people as well as their culture. In essence, this 'Okhotsk expansion scenario' suggests that, far from being direct descendants of a single ancient human lineage that had no contact with the rest of the world, the Ainu and their culture are the outcome of a recent population expansion into northern Hokkaido.

If we accept premises (i) population expansions often leave its signature in the patterns of linguistic variation and (ii) the cultural flow from the incoming Okhotsk people had a profound impact on the language, then we can reason that spatiotemporal reconstruction of the Ainu language evolution might allow us to test the plausibility of the Okhotsk expansion scenario for the Ainu origin, and

examine whether or not the dual-structure model should be modified to accommodate the Okhotsk expansion scenario. Accordingly, it was predicted that if the scenario were correct, then the estimated root age of the Ainu variants should coincide with 900 - 1,600 BP (Hanihara, 2010), and their geographic distribution should be the end result of expansion from northern Hokkaido, where the gene and cultural flows from the Okhotsk to Jomon is likely to have taken place (blue bar in figure 2.1). Following the line of reasoning above, it was also predicted that if the scenario were incorrect, then the Ainu language diffusion should conform to the conventional scenario and spread northward from southern Hokkaido with the root age around 10,700 BP (Turner, 1986).



**Figure 2.1 Map of the Ainu language variants.** Coloured circles represent two major subgroups (Green-Hokkaido; Yellow-Sakhalin). Blue bar in the center indicates the area of the Okhotsk settlement.

#### 2.2. Materials and methods

The data consist of 19 geocoded lists of 200 basic vocabularies compiled by Hattori and Chiri during 1950s, when there was still a rich linguistic diversity among the Ainu people (Hattori & Chiri, 1960). The basic vocabularies are a set of words transmitted vertically from one generation to the next (Embleton, 1986), thereby preserving evolutionary signal required for reconstructing phylogenetic history (Greenhill, Blust, & Gray, 2008; Pagel, 2009). Nevertheless, one could argue that the 19 variants that I analyse here are dialects of the Ainu language, and if one supposes that only languages, not dialects, constitute representative units of analysis, then using these variants implies that the resulting tree may potentially depict a confusing branching pattern with excessive detail, or even fail to recover the actual subdivisions of the speech community (Crowley & Bowern, 2009).

I do not, however, consider this to be a major obstacle for reconstructing Ainu language evolution for three reasons: (i) a natural model of language evolution that I use here is known to be robust against reasonable levels of noise in the dataset (i.e., up to 20% of horizontal transfer per 1,000 years) (Greenhill, Currie, & Gray, 2009), (ii) if languages are defined as groups of tongues that are mutually unintelligible in a manner similar to biologists defining species as groups of animals that cannot interbreed (Pagel & Mace, 2004), then Swadesh's criterion of mutual intelligibility [i.e., any two languages being mutually unintelligible if they share less than 90% of their basic vocabularies with each other (Swadesh, 2006)] and a matrix of pair-wise cognate similarities of the Ainu variants (Hattori & Chiri, 1960) lead to the estimation that any one of the variants would be able to communicate with the rest only about 18% on average, meaning that the majority of the 19 variants can actually be considered languages in their own right, and (iii) I used SPLITSTREE4 (Huson & Bryant, 2006) to estimate tree-likeness of the

Ainu phylogeny (Gray, Bryant, & Greenhill, 2010; Holland, Huber, Dress, & Moulton, 2002) and obtained the average delta score = 0.25 and *q*-residual score = 0.01, both indicating that the evolution of Ainu lexicons was reasonably tree-like, and hence suitable for phylogenetic analysis. Putting this in perspective, the tree-likeness scores calculated from a subset of 12 Indo-European languages have similar scores as the current 19 Ainu variants with the average delta score = 0.23 and *q*-residual score = 0.03 (Gray et al., 2010). These observations provide enough evidence to assume that the data should carry robust evolutionary signal, and the 19 Ainu variants are appropriate units of analysis for the current purpose.

Cognate judgments, a process of revealing shared ancestry among lexicons, are typically carried out by identifying systematic correspondences in phonetic structure and meaning (Crowley & Bowern, 2009). For the current analyses, I adopted the cognate judgments made by the two linguists who compiled the data (Hattori & Chiri, 1960). The cognate sets were encoded into binary states indicating presence ('1') or absence ('0') of a cognate, which resulted in 19 × 350 matrix.

I used BEAST (Drummond, Suchard, Xie, & Rambaut, 2012) for all analyses because it allows reconstruction phylogenies without specifying an *a priori* outgroup. Continuous random walk model used in this study (Lemey et al., 2010; Pybus et al., 2012) is a Bayesian expansion of Brownian diffusion model developed in a maximum-likelihood framework (Lemmon & Lemmon, 2008). In general, a Brownian diffusion model aims to estimate the vectors of latitudes and longitudes of internal nodes (i.e., common ancestors of extant languages) on a continuous surface, in which increments are independent and normally distributed with a mean centred on zero with variance that scales linearly in time, meaning that diffusion processes are assumed to be homogeneous over time and space. This can be unrealistic as many geographic features (e.g., mountains and rivers) can

influence the rate of spread for each branch. Bayesian continuous diffusion model I adopt here effectively overcomes this limitation by relaxing the Brownian process: borrowing ideas from uncorrelated relaxed clock models (Drummond, Ho, Phillips, & Rambaut, 2006), the method models branch-specific dispersal processes with a diffusion rate scalar in each branch being drawn independently and identically from a range of parametric distributions. The parametric distributions used in the current analyses are (i) Cauchy distribution that has fat tails accommodating long distance dispersals (Paradis, Baillie, & Sutherland, 2002), (ii) gamma distribution that accommodates infinite variance in a manner similar to Lévy flight models (Reynolds & Rhodes, 2009) but without enforcing power-law tail behaviour, and (iii) lognormal distribution that allows even greater degree of rate variability (Drummond et al., 2006). In order to make the geographic inference more realistic, I sampled the root and node locations only from the land by assigning a prior probability of zero to the water (Bouckaert et al., 2012).

In addition, I compared the degree of model-fit between relaxed and strict clocks (Drummond et al., 2006). Temporal scale of phylogenies was calibrated using a probabilistic prior taken from well-attested evidence that modern Ainu expanded into Sakhalin around 15th century (Ishida & Kida, 1991; Ohyi, 1985): a normallydistributed prior with a mean of 500 BP with its 95% of the distribution incorporating 200 years of uncertainty. For all analyses, I applied a stochastic Dollo model with a correction for ascertainment bias (Alekseyenko, Lee, & Suchard, 2008) and a Bayesian skyline tree prior (Drummond, Rambaut, Shapiro, & Pybus, 2005). I chose the best model by comparing Bayes Factors (BF) (Baele et al., 2012).

**Table 2.1 Log-marginal likelihoods estimated from all models fitted to data.** The model with a relaxed clock and gamma-distributed random walk model shows the best fit with the highest log-marginal likelihood.

<b>Diffusion models</b>	<b>Relaxed</b> clock	Strict clock
Homogeneous Brownian	-2364.20	-2368.69
Cauchy	-2367.58	-2375.33
Gamma	-2362.93	-2369.06
Lognormal	-2365.46	-2374.05

### 2.3. Results

Based on BF tests among diffusion models and evolutionary clock models, I chose the relaxed clock with gamma-distributed diffusion as the best model (table 2.1). Figure 2.2 shows the summary of time-dated maximum clade credibility trees for 19 Ainu language variants. It was predicted that if the recent evidence supporting the Okhotsk expansion scenario were correct, then the estimated root age should overlap with 900 - 1,600 BP. The estimated root age of the Ainu language across post-burn-in trees has a median of 1,288 BP [mean: 1,323 BP; 95% Highest Posterior Density (HPD): 820 - 1,862 BP], in strong agreement with the prediction.



**Figure 2.2 Maximum clade credibility tree of 19 Ainu language variants.** Coloured branches represent two major subgroups (Green-Hokkaido; Yellow-Sakhalin). All node heights are scaled to match the posterior median node heights with bars indicating 95% HPD intervals of the estimated ages. The value on each branch is the posterior probability, showing the percentage support for the following node.

It was also predicted that if the hypothesized scenario were correct, then the current distribution of 19 Ainu language variants should be the end result of diffusion from northern Hokkaido; otherwise, the diffusion pattern should show northward expansion from southern Hokkaido, conforming to the conventional dual-structure model. Figure 2.3 shows that the estimated diffusion pattern in natural time scale (Bielejec, Rambaut, Suchard, & Lemey, 2011) is in clear agreement with the prediction, with the estimated homeland being in northern Hokkaido. Both the diffusion pattern and root time were consistent across all models I excluded based on BF tests, and using a time-reversible model yield almost identical results as the stochastic Dollo model.



**Figure 2.3 Inferred origin and diffusion of the Ainu language variants in natural time scale.** Colour gradient of the polygons (80% HPD) indicates relevant age of the diffusion [Blue-older (1,288 BP); Red-more recent (50 BP)]. White lines represent the phylogeny projected onto the surface. Image sources: © 2012 Google Earth; © 2012 Cnes/Spot Image; © 2012 TerraMetrics.

In order to examine the robustness of the phylogeographic inferences, I carried out two additional tests. Firstly, I tested the strength of support for northern Hokkaido origin (i.e., the Okhotsk expansion scenario) over southern Hokkaido origin (i.e., the dual-structure model) by directly calculating BF: Hokkaido was divided into two broad regions of north and south at the centroid of Hokkaido, and BF was estimated by comparing the posterior to prior odds ratio of observing potential homeland in either one of the two regions. In agreement with the results presented above, the test yielded substantial support (BF=7.5) for northern Hokkaido being the homeland of the Ainu.

Secondly, I investigated whether or not the results are statistical artefacts of the diffusion model falling into the centre of language mass regardless of the data: the locations of 19 Ainu variants were randomly assigned to the data for fifty times, and then obtained 90% HPDs for all possible root locations (figure 2.4). This exercise demonstrated that the absence of true signal could cause the estimated homeland to be as south as mainland Japan or as north as Sakhalin. This observation clearly demonstrates that the current results are valid estimations based on true phylogeographical signal. Conversely, this also suggests that if the data contained signal indicating northward diffusion, or any other direction, the methods adopted here would have reconstructed it accordingly.



**Figure 2.4 Ninety percent highest probability density obtained from fifty random reassignments of location coordinates to the tips of phylogeny.** This demonstrates that the current results are not statistical artefacts of the diffusion model returning to the center of language mass. For all analyses, an arbitrary root calibration was applied which consisted of a normal distribution with the mean of 1,500 BP and the standard deviation of 400 years. I acknowledge, however, that a well-established subgroup of the Ainu language, namely the Kuril, is absent from the data. This is because the Kuril had become extinct by the time the data were collected, and the Kuril lexicons seem to be available only through sketchy records scattered around the literature. For this reason, there is currently little information available about the Kuril. If the point in time that the Kuril diverged from other variants turns out to be much deeper, then the resulting divergence time and diffusion pattern may differ significantly from the current results. The search for a more complete set of data is, therefore, a direction that should be prioritized for further evaluation of the conclusion I made here.

### 2.4. Discussion

In this chapter, I reconstructed spatiotemporal evolution of 19 Ainu language variants, and the results were in strong agreement with the hypothesis that a recent population expansion of the Okhotsk people played a critical role in shaping the Ainu people and their culture. Together with the recent archaeological, biological and cultural evidence, the phylogeographic reconstruction of the Ainu language strongly suggests that the conventional dualstructure model must be refined to explain these new bodies of evidence. The case of the Ainu language origin reported here also contributes additional detail to the global pattern of language evolution, and the current language phylogeny might also provide a basis for making further inferences about the cultural dynamics of the Ainu speakers (Currie, Greenhill, Gray, Hasegawa, & Mace, 2010; Mace & Jordan, 2011).

I recognize that there are also some evidence that the Jomon people, one of the two ancestral populations of the Ainu, may have descended from Northeast Asia rather than Southeast (Adachi et al., 2011; Hanihara & Ishida, 2009), thereby questioning the validity of dual-structure model on a greater time scale. Unfortunately, the scope of the results presented here have little bearing on the larger question of the Jomon prehistory because the linguistic traces of this process may have been wiped out by the recent rise of the Ainu as the results indicate. Regardless of what further research reveals about the Jomon ancestry, however, I argue that the evidence for the Okhotsk expansion scenario should remain valid, and therefore any future models of deeper historical process for the Japanese islands must properly account for the recent northern Hokkaido origin of the Ainu. With this respect, I suggest that the most effective way of shedding light on the deeper history of the Jomon, or historical processes of any other regions, is to synthesize different lines of evidence from archaeology, biology and culture, and triangulate them to obtain a rigorous analytic framework (Gray et al., 2007) rather than relying on a single line of evidence (Jinam et al., 2012).

If the inferences are correct, then the recent Okhotsk expansion scenario for the Ainu origin leads to a new question: what historical factors drove the Okhotsk people to migrate from the Amur river basin to Hokkaido and give rise to the Ainu? It is now clear that early farming populations went through similar processes due to agricultural intensification and cultural innovation (Diamond & Bellwood, 2003) but the Okhotsk people were hunter-gatherers, not farmers. While not resolving this question directly, Hudson (2004) provides a comprehensive model of the Okhotsk socio-environmental conditions that leads to a possible scenario: (i) the diet of the Okhotsk people relied heavily on marine mammal products and (ii) the time in which the Okhotsk expansion occurred seems to be characterized by dramatic climate changes, beginning with a cold seaice stage between 1,300 - 1,800 BP followed by a warmer open-ocean stage. Based on these observations, I speculate that the Okhotsk expansion may have been opportunistic in nature: the sea-ice condition in the early stage probably resulted in increased area for exploiting marine mammals as well as convenient routes for

exploring new territory, thereby leading to the migration into Hokkaido. The drastic climate change in the later stage, however, may have deteriorated the hunting conditions for the Okhotsk with rapid break up of sea-ice, which may also have necessitated increased reliance on other types of food source, and hence causing a greater degree of niche overlap with the preexisting Jomon population. The end result was probably the admixture of the two populations, followed by the rise of a new ethnolinguistic group, namely the Ainu.

If we accept a view that transmission of language may be gender-specific (Forster & Renfrew, 2011; Quintana-Murci et al., 2001; Wen et al., 2004), then it is possible to formulate at least two hypotheses for the specific processes of the Ainu language origin. Because Y-chromosome haplogroup D is thought to represent Jomon male ancestry, the predominance of that particular haplogroup in the Ainu (75 - 87.5%) implies that the majority of Ainu male ancestry is from the Jomon (Hammer et al., 2006; Tajima et al., 2004), whereas a heavy mixture of mtDNA haplogroups indicates that a significant proportion of the Ainu female ancestry is from the Okhotsk [excluding 35.3% of mtDNA haplogroups that the Ainu share with other neighbouring populations, 39.4% of the remaining female heritage is shared exclusively with the Okhotsk and the rest is a mixture of both Jomon and Okhotsk (Adachi et al., 2011; Sato et al., 2009; Tajima et al., 2004)]. If we thus assume male-specific language transmission for the Ainu, the first hypothesis for the processes behind the Ainu language origin could be that proto-Ainu arose from a large number of Jomon males who intermarried with Okhotsk females in northern Hokkaido, and subsequently spread to the rest of region. Similarly, if we assume that the transmission of Ainu language corresponds with female ancestry, the second hypothesis could be the incoming Okhotsk females who merged with the preexisting Jomon males spoke that proto-Ainu. Based on these observations, I propose that one potential way of understanding how language change occurred for the Ainu is to estimate which gender was more

influential when early Ainu people established family membership. This may be carried out indirectly by revealing the signature of historical post-marital residence pattern via estimating the degrees of genetic variation in their Ychromosome and mtDNA (Oota, Settheetham-Ishida, Tiwawech, Ishida, & Stoneking, 2001) as well as reconstructing ancestral post-marital residence rules from regional cultural variation (Jordan, Gray, Greenhill, & Mace, 2009). Investigating which model of language change (Renfrew, 1989) is relevant to the Ainu is a direction that deserves more attention, and acquiring an accurate description of how language change occurred for the Ainu would enable further inferences about the deeper history of the human lineage that once thrived in northern Japan.

Languages rise and fall, and so do the communities who speak them. Although significant progress has been made in recent years, we are still far from thoroughly understanding why languages are so deeply related to the fates of their speakers or how the process unfolds through evolutionary history. These are perhaps some of the most challenging questions in human sciences, and a complete understanding of this complex phenomenon might thus be reached only with further methodological innovations as well as more language data from around the world. But as I demonstrate in this study, a combination of spatiotemporal reconstruction of language evolution and synthesis of several different historical evidences is probably one of the most promising methodologies that can further illuminate the process and consequence of this fascinating phenomenon.

### **Chapter Three**

## Bayesian inference of Japonic language phylogeny: a closer inspection<sup>2</sup>

W.S. Holt once remarked that history is "a damn dim candle over a damn dark abyss". I previously attempted to shed light on the evolutionary history of 59 Japonic languages by demonstrating that the root age of these languages was closely bound with the migration of agricultural population around 2,500 years ago. Together with archaeological and biological evidence, I also argued that the estimated root age implied that the first farmers of Japan had a profound impact on the origins of both people and languages in the Japanese Islands. However, a number of criticisms were raised against the data and methods used in this study, which created a barrier to a wider acceptance of the results. In this chapter, I recapitulate the main findings from the analysis on Japonic language family, and then review some of the major points made by the critics, followed by attempts to address the criticisms. While the study of human prehistory with language evolution is indeed a daunting task, I argue that none of the criticisms are strong enough to discredit the conclusion made from Bayesian inference of Japonic language phylogeny.

<sup>&</sup>lt;sup>2</sup> This chapter is based on Lee, S., & Hasegawa, T. (2011). Bayesian phylogenetic analysis supports an agricultural origin of Japonic languages. *Proceedings of the Royal Society of London B Biological Sciences*, 278(1725), 3662–3669. doi:10.1098/rspb.2011.0518 and several invited talks since the publication of the article.

<sup>&</sup>lt;sup>3</sup> Holt, W. S. (1933). Treaties defeated by the senate. Baltimore: Johns Hopkins Press.

# 3.1. A phylogenetic approach to language change and variation

Significant controversy surrounds prehistoric processes that shaped the patterns of linguistic diversity. This controversy is an outcome of numerous contributing factors, but the major barrier that impeded scholars from reaching a consensus was the lack of suitable methodology that can precisely quantify the dynamics of linguistic diversity. Early attempts to grasp the patterns of linguistic diversity such as lexicostatistics and glottochronology could not survive scientific scrutiny because they not only failed to distinguish shared-innovations from shared-retentions, but also misconceived that the rates of linguistic change are universally constant. Consequently, these methods were often found to produce misleading divergence time estimation and tree topology for various language families (Bergsland & Vogt, 2010; Blust, 2000).

Fortunately, recent progress in phylogenetic methods shows promising signs that the statistical techniques developed for studying biological evolution can provide adequate solutions for these problems (Atkinson & Gray, 2005). Accumulating empirical evidence suggests that languages have, surprisingly, gene-like properties in many aspects, and they too evolve by a process of descent with modification (Pagel, 2009). This implies that once the shared-innovations among languages are revealed in the form of cognate (Crowley & Bowern, 2009), various stochastic phylogenetic techniques for modelling biological evolution can be used to infer the history of language change and variation. During the last decade, therefore, these techniques have been quickly adopted to reconstruct the evolutionary history of Bantu (Holden, 2002), Indo-European (Bouckaert et al., 2012; Gray & Atkinson, 2003), and Austronesian languages (Gray & Jordan, 2000; Greenhill & Gray, 2009). Accordingly, I took advantage of these methodological breakthroughs to reconstruct the evolutionary history of Japonic languages, and examined the plausibility of farming/language coevolution hypothesis (Diamond & Bellwood, 2003), which predicts that Japonic languages originated from an ancient language spoken by prehistoric farmers who migrated to the Japanese Islands around 2,500 years ago (Hudson, 1999). It was hypothesized that if the recent farming population were responsible for shaping the diversity of Japonic languages, then the time depth of Japonic origin would be located within 1,700 - 3,000 years before present (BP) (Hudson, 1999). An alternative hypothesis was also formulated, which predicts that if much older Pleistocene hunter-gatherer population, rather than the farmers, made the majority of contribution to the linguistic diversity in the Japanese Islands, then the time depth may be found within anywhere between 12,000 - 30,000 BP (Suzuki, 1981). Figure 3.1 shows the sampling locations of the languages used for the analyses.



**Figure 3.1 Map of Japonic languages.** Subgroups are coded with colour circles: yellow, eastern Japanese; orange, western Japanese; red, Hachijyo; blue, Kyushu; purple, northern Ryukyuan; pink, southern Ryukyuan.
In order to estimate the root divergence time, the posterior probability distribution of Japonic language phylogenies was inferred using (i) 59 lists of 210 basic vocabularies extracted from multiple sources (Hirayama, 1988; 1992; Jōdaigo Jiten Henshū Iinkai, 1967; Muromachi Jidaigo Jiten Henshū Iinkai, 2001), (ii) calibration priors assigned to Old and Middle Japanese with log normal priors (97.5% of the distributions lying between 1,215 - 1,300 BP and 437 - 674 BP respectively) as well as a probabilistic divergence time prior to Tokyo and Kyoto (407 BP with the standard deviation of 135.2 years) (Clarke, 1989), and (iii) a relaxed clock (Drummond et al., 2006) with covarion model (Penny, McComish, Charleston, & Hendy, 2001).



**Figure 3.2 Maximum clade credibility tree of Japonic languages.** All node heights in the tree are scaled to match the posterior median node heights. The value on each branch of the tree is the posterior probability, showing the percentage support for a node following a particular branch. Posterior probabilities below 50% are not shown. The green bar represents the age range predicted by the farming/language theory (1,700 – 3,000 BP).

## 3.2. Bayesian inference of Japonic language phylogeny

It was predicted that if the origin of Japonic languages were indeed related to the advent of prehistoric farmers, then the estimated time for the root would be found within 1,700 and 3,000 BP. In contrast, the alternative hypothesis predicted that the root would be found anywhere between 12,000 and 30,000 BP. As figure 3.2 shows, the median age of the root is estimated to be 2,182 BP [mean: 2,398 BP; standard error: 47.21 years; 95% Highest Probability Density (HPD): 1,239 - 4,190 BP], which is clearly in agreement with the scenario that the prehistoric farmers had a profound impact on the origin of Japonic language family. The Japonic language tree correctly recovers the expected major subgroups of Ryukyuan and mainland Japanese as well as minor subgroups such as northern Ryukyuan, southern Ryukyuan, Kyushu and most of western Japanese. In addition, the posterior probabilities for branches older than 500 BP are high (i.e., above 70%), and these indicate that deeper relationships of Japonic languages.



Figure 3.3 Histogram of the estimated time for the root of Japonic languages.

Green bar represents the age range predicted by the farming/language coevolution hypothesis and grey bar represents the age range predicted by the alternative hypothesis. The median root divergence time is 2,182 BP and the mean is 2,398 BP with the standard error of 47.21 years. The 95% highest probability density is 1,239 - 4,190 BP. Based on these results, I concluded that the history of Japonic languages is deeply related to the agricultural population; but a number of criticisms have been raised against the data and methods used in this study. Thus, here I review some of the major criticisms, and attempt to answer them appropriately.

## 3.3. Criticisms and responses

#### 3.3.1. How reliable is the model?

An unrefined criticism that has frequently been raised against the time-dated Japonic language tree is that the results are a statistical artefact from a carefully orchestrated model setting. It is unfortunate, however, that the critics fail to grasp that no serious phylogeneticists would report their results without carrying out some model selection procedures. More specifically, the results from the relaxed clock with covarion model was reported because simply the model had the best projection for the evolutionary processes of Japonic languages among four different evolutionary models, as determined by importance sampling and Bayes factor test (Suchard, Weiss, & Sinsheimer, 2001). Obviously, the model selection procedure disregards the investigator's subjective bias, and thus precludes the possibility of producing artificial results. In order to show the rigorousness involved with model selection, descriptions of the way in which each model projected the evolutionary process of Japonic languages are provided below.

The first model used a strict clock model with an eight-category gamma correction of rates (STRICT+ $\Gamma$ ). This model assumes that rate variation between languages is relatively constant through a strict clock model, but variable within languages with gamma correction. The gamma correction assigns different rates of evolution across cognates by giving slow rates for rarely appearing cognate sets and fast rates for frequently appearing sets with a parameter alpha ( $\alpha$ ) (Yang, 1996). Under the gamma correction, the rates across languages are maintained from the time of origin to the present. The second model also applied the gamma

correction, but in adjunction with an uncorrelated lognormal relaxed clock model (UCLD+ $\Gamma$ ) rather than a strict clock. Under the relaxed clock model, rate variation between languages is corrected by assigning different rates (which are drawn from a lognormal distribution) to different languages (Drummond et al., 2006). Therefore, coupled with the gamma correction that accommodates for within-language rate variation, this model explores the possibility of rate variation both between and within languages. The third model assumed the covarion model in addition to the strict clock model (STRICT+Cov). This model assumes that the evolutionary rate is relatively constant between languages with the strict clock model but it could be different within languages with the covarion approach, which assumes rate variations between languages as well as within languages; but unlike the models using the gamma correction, the rate is allowed to switch between fast or slow ones during evolution. This is achieved by incorporating two parameters into the model: Phi ( $\varphi$ ), which allows some proportion of sites to vary freely and Delta ( $\delta$ ), which allows some sites to switch between variable and invariable sites (Penny et al., 2001). In other words, the covarion approach assumes that most cognate sets evolve neutrally; and there are some cognate sets that do not vary at all; but at the same time, the invariant sets can become variable sets over the course of time and vice versa. The fourth model, which was chosen as the best fit for the data, was based on the relaxed clock model with the covarion approach (UCLD+Cov).

The detailed descriptions of all models involved in the model selection procedure clearly show that each model is firmly rooted in stochastic theories of evolution, and the best model was not arbitrarily formulated to produce desired outcome. Additionally, table 3.1 shows that the root ages estimated from all four models are remarkably similar, which demonstrates that if we focus only on the 95% HPDs, then the models that ended up being discarded actually show better fit for the age range predicted by farming/language hypothesis (probably due to ignoring rate

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variability among language variants). Based on these observations, it should be clear that the claim of the results being a chance result is nonsense.

# Table 3.1 Summary of root age estimations obtained from all four models. ${\rm All}$

numbers indicate years before present.

	Mean	Median	95% HPD lower boundary	95% HPD upper boundary
<b>STRICT</b> + $\Gamma$	2670.02	2629.87	2052.45	3367.58
<b>UCLD</b> + Γ	2449.50	2420.25	1950.36	3014.25
STRICT+Cov	2341.74	2193.71	1231.99	3847.11
UCLD+Cov	2393.98	2181.78	1239.21	4189.66

3.3.2. How robust is the result against horizontal transfer? More informed critics correctly point out that a potential problem with any phylogenetic approach, regardless of whether it is applied to linguistic or biological data, is horizontal transmission. This is particularly problematic because despite the study's best effort to remove all borrowings from the data, there is no guarantee that every single borrowing has been filtered out from the dataset. Fortunately, a recent simulation study demonstrates that the amount of undetected borrowing needs to be unrealistically high to invalidate divergence time estimation or tree topology (Greenhill et al., 2009). The study compared normalised quartets distances between artificially simulated tree topologies, and reconstructed trees from multiple datasets in which the amount of horizontal transfer was systematically manipulated. Through rigorous comparisons, it was observed that the amount of horizontal transfer should be greater than 20% per 1,000 years to invalidate phylogenetic reconstructions, which is considered extremely unlikely by many scientists (Bowern et al., 2011). Thus, I argue that Bayesian inference of Japonic language phylogeny would withstand some amount of undetected horizontal transmission that may or may not exist in the data. At the same time, however, it should be acknowledged that high levels of horizontal transmission are known to have occurred in a few rare instances (Haspelmath & Tadmor, 2009). Hence, if this is also the case for the current dataset then the results would be seriously affected; but unless the amount of horizontal transfer is formally quantified for Japonic language family and demonstrated to be greater than the threshold, I maintain the position that this is an unlikely event.

#### 3.3.3. Flawed testing framework?

Another criticism made by the critiques is that the method used in this study may not accurately distinguish between two hypotheses, because the proposed time depth of the competing alternative hypothesis (i.e., 12,000 - 30,000 BP) lies

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beyond the limit that many linguists consider recoverable from linguistic data (8,000 - 10,000 BP). However, it should be noted that the supposed limit is estimated under an assumption that all words evolve at the same rate (Ringe & Donald, 1995), which is unlikely for the majority of language families (Bergsland & Vogt, 2010; Blust, 2000). A recent work suggests that a more realistic model of cognate evolution, which is similar to the models used here, allows linguistic ancestry to be detected even after 20,000 years (Pagel, 2000). Furthermore, a subset of basic vocabularies has recently been demonstrated to contain robust historical signal that can be traced back to 15,000 BP (Pagel, 2013). Therefore, if the current data had any signals indicating deep evolutionary relationships in support of the competing alternative hypothesis, then the method would have accurately reflected such signals to the node heights, meaning that the testing framework proposed here is far from being flawed.

3.3.4. Test of reliability: an independent replication It was reasoned that the best argument that could be made against the three criticisms described above would be an independent replication of the time-dated phylogeny, in a manner similar to replication being the best strategy for confirming the validity of experimental findings. Thus, another set of analyses was carried out with a small but independent set of Japonic language data (Starostin, Dybo, & Mudrak, 2003). Some scholars point out that Starostin's data is considered controversial, as Starostin made debatable reconstructions of proto-Japonic and used them to argue for genetic relationships to other equally debatable proto-languages such as proto-Tungusic. However, this is not a serious obstacle for reproducing time-dated Japonic phylogeny, as those controversial reconstructed lexicons are simply discarded from the analyses.

The data consisted of 110 basic vocabulary lists on 9 Japonic languages, and after the cognate sets were converted to binary codes, a series of model testing was

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conducted. The maximum clade credibility tree from the best fitting model, which was STRICT+ $\Gamma$ , indicates that the median root divergence time is 1,976 BP (the mean: 2,080 BP; the standard error: 9.13 years; 95% HPD: 1,232 - 3,279 BP) clearly in agreement with the results from the larger dataset (figure 3.4).



**Figure 3.4 Maximum clade credibility tree of 9 Japonic languages.** Subgroups are coded with colour circles: yellow, Eastern Japanese; orange, Western Japanese; blue, Kyushu; purple, Northern Ryukyuan; pink, Southern Ryukyuan. Green bar represents the age range predicted by the farming/language dispersal theory (1,700 - 3,000 BP).

3.3.5. Absence of language diversification in the initial stage? Some critiques pointed out that the estimated Japonic phylogeny indicates that the arrival of the farmers did not necessarily lead to a burst of language diversification, in contrast to other language families that experienced a similar history (i.e., population expansion) often showing a series of short branches from the root leading to the tips. This demands an explanation because (i) soon after their arrival, the proto-Japonic farmers were already divided into several chiefdom-like political units fighting each other to gain access to resources, as indicated by archaeological evidence of defensive moats surrounding settlements, arrowheads, and skeletons damaged by sharp objects (Nakahashi, 2005) and (ii) a fully-fledged centralized government makes its first appearance about 1,000 years after the arrival of the farmers: the Nara era that spoke Old Japanese. If it is correct to assume (i) that languages separated by political barriers may take different evolutionary paths (Hock, 1986) and (ii) that political power in Japan remained fragmented for a long time, then there could have been more linguistic diversity in the early Japan. A data source that was used to extract Old Japanese lexicons (Jodaigo Jiten Henshū Iinkai, 1967) also indicate that there could have been some linguistic variations in the Nara era.

The fates of those ancient languages are unknown at present, if there were any. There are two possibilities. One possibility is that the early linguistic diversity could have been wiped out with the emergence of a strong centralized political power in the Nara era, and hence leaving no traces behind. The other possibility is that the early chiefdom-like political units were not able to maintain their states long enough to give rise to any detectable language splits. Further research would be required to clarify this matter. It should be noted, however, this criticism cannot in itself invalidate the Japonic language phylogeny, as it is merely emphasising the current state of knowledge that there are many more unanswered questions regarding the prehistory of Japonic languages.

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3.3.6. Why difference in the evolutionary patterns between subgroups? Perhaps the most difficult issue to deal with is the reason why node supports are noticeably lower among mainland Japanese variants (i.e., below 70%) than among Ryukyuan variants. This is a hard question to answer partly because the issue concerns with yet unknown process of Japonic language evolution, when the current focus has been on inferring the pattern of Japonic language evolution. As it was mentioned in Introduction, the pattern and process of evolution are two separate dimensions of a phenomenon that deserve individual examination (Sober, 1991).

I suggest that the process leading to this pattern may be hypothesized at two levels of causation: proximate and ultimate. At the proximate level, low node supports among variants occurred because the isoglosses that separate variants are small and they do not overlap together, therefore the tree-building algorithm ended up exploring several possible subgrouping patterns with similar probabilities (Crowley & Bowern, 2009). This also means that the relationships within mainland Japanese variants are non-tree-like, which its extent can be visualized with NeighborNet analysis (Huson & Bryant, 2006), as shown in figure 3.5.





content distances were used and splits were filtered to a threshold of 0.001. Reticulations indicate presence of conflicting signals. Scale bar: 0.01.

It might be expected that under the 'dialect chain formation/break-up' model of lexical evolution (Gray et al., 2010) in which the intermediate dialect chains would be pruned and produce tree-like linguistic relationship as a function of time (Garrett, 2006), one would expect to see more or less the same amount of reticulations from both mainland Japanese and Ryukyuan variants, as they are both descendants of a 2,200-year-old common ancestor. However, split graphs in figure 3.5 seem to suggest that mainland Japanese on the left side has a significantly higher level of conflicting signals than Ryukyuan on the right.

Based on this observation, I hypothesize that one of the ultimate causes for relatively low node supports among mainland Japanese variants may be the difference in the degree of internal linguistic contact (Hock, 1986) within mainland Japanese and Ryukyuan. An obvious difference between the two groups is that whereas each Ryukyuan variant is contained within a geographically isolated island, mainland variants are connected to their neighbours via land routes. Thus, the lack of geographical barriers might have slowed down the pruning process among mainland Japanese variants (either by allowing horizontal transmission or complex population diffusion) and this could potentially be the cause of low node supports for that part of the tree. The validity of this hypothesis is fully investigated in the next chapter.

## 3.4. Conclusion

In this chapter, I recapitulated previous findings on Japonic language evolution, and reviewed some of the major criticisms against the data and methods that were used to argue for farming/language coevolution. While I claim that none of these criticisms are sufficiently strong to discredit the conclusion, I must acknowledge that I am merely holding a damn dim candle over a damn dark abyss, and hence a full understanding about how linguistic mutations arise, accumulate, and give birth to different languages in the Japanese Islands lies in the future.

Perhaps further questions regarding Japonic language phylogeny might be addressed by incorporating information about typological variation into phylogenetic analysis. It has been suggested that there is a considerable structural (phonological and grammatical) variation among Japonic languages, which appears to be more noticeable for Ryukyuan group than mainland Japanese group (Shibatani, 1990; Shimoji & Pellard, 2010). If typological variation of Japonic languages contain enough historical signal, then it is indeed possible that they can contribute to a better understanding of Japonic language history, similar to previously demonstrated cases of Austronesian languages (Dunn, Levinson, Lindström, Reesink, & Terrill, 2008; Dunn, Terrill, Reesink, Foley, & Levinson, 2005). It is unlikely that all typological variations will be informative since such a property as word order has no variation among Japonic languages, with all languages having subject-object-verb for transitive sentences; but properties such as accent or tone appear to display enough variation to be incorporated into phylogenetic analysis (Shibatani, 1990; Shimoji & Pellard, 2010). Although further research is required to identify the precise structural features that are informative in studying language evolution (Dediu & Levinson, 2012; Greenhill, Atkinson, Meade, & Gray, 2010a), taking a more holistic approach to quantifying language

evolution is a direction that might provide more answers to remaining questions about Japonic language history.

Recent findings on language evolution may also provide further clues about the evolutionary processes that shaped linguistic diversity in the Japanese Islands, or even on a global scale: languages tend to evolve in a punctuational burst-like manner following speciation events (Atkinson, Meade, Venditti, Greenhill, & Pagel, 2008); frequency of word-use in everyday speech contributes to evolutionary rate heterogeneity within languages (Pagel, Atkinson, & Meade, 2007); and both drift-like process (Reali & Griffiths, 2009) as well as adaptation (Kirby, Cornish, & Smith, 2008) seem to regulate vertical transmission of language from a generation to the next. With these parallel properties between biological and linguistic evolution, I remain hopeful that a Darwinian framework holds great promise for further elucidating the intertwined history of physical replicators like our genes and nonphysical replicators like our languages.

# 3.5. Appendix

Cognate judgments were made by (i) consulting previously identified sound correspondences that were used for internal reconstruction of proto-Japonic [e.g., (Frellesvig & Whitman, 2008; Whitman, 1985)], (ii) working out systematic sound correspondences based on comparative method (Crowley & Bowern, 2009), and (iii) consulting previously published cognate judgments on Japonic languages (Hattori, 1961; 1978-1979).

As Ryukyuan and mainland Japanese are two major branches of Japonic family, sound correspondence examples presented here are mainly those between mainland Japanese and Ryukyuan. No assumptions were made about the direction of change between words. Thus, the regular sound correspondences were made strictly based on the currently observable states, without considering reconstructed/transitional states between words. Examples of sound correspondences are as follows.

Mainland Japanese (MJ)	Ryukyuan (R)	Corresponding words
/k/ preceding vowel /u/	/F/ preceding vowel /u/	kusa (MJ) : Fusa (R) 'grass'
		kusa- (MJ) : Fusa (R) 'rotten'
		kut∫i (MJ) : Fut∫i (R) 'mouth'
/e/ after consonant	/i/ after consonant	ke (MJ) : ki (R) 'hair'
		ame (MJ) : ami (R) 'rain'
		te (MJ) : ti (R) 'hand'
/o/	/u/	kiːro (MJ) : kiːru (R) 'yellow'
		omo- (MJ) : umu (R) 'to think'
		kokono-(MJ) : kukunu-(R) 'nine'
/u/ after consonant /t∫/	/i, ï/ after consonant /t∫/	tsuki (MJ) : tsï- (R) 'moon'
		itsutsu (MJ) : itsïtsï (R) 'five'
		çitotsu (MJ) : p <sup>s</sup> ïti I tsï (R) 'one'
/k/ before vowel /i/	/ts, t∫/ before vowel /i/	ki- (MJ) : ts-, t∫- (R) 'to hear'
		ki- (MJ) : ts-, tf- (R) 'fog'
		ki- (MJ) : ts-, t∫- (R) 'to cut'
medial /m/	medial /b/	kemuri (MJ) : kibu-,kipu- (R)
		'smoke'
		sema- (MJ) : seba- (R) 'narrow'
initial /h/	initial /p/	hane (MJ) : pani (R) 'wing'
		hana (MJ) : pana (R) 'flower'
		hana (MJ) : pana (R) 'nose'
initial /j/	initial /d/ (Yonaguni)	jaku (MJ) : dakuN (Yonagni) 'to
		burn'
		jaQt∫u (MJ) : dat∫i (Yonaguni)
		'eight'
initial /w/	initial /b/	wa- (MJ) : ba- (R) 'I'
		wa- (MJ) : ba- (R) 'We'
		war- (MJ) : bar- (R) 'to laugh'

## Table 3.2 Sound correspondences between mainland Japanese and Ryukyuan.

# **Chapter Four**

# Geographical isolation promotes language diversification in the Japanese Islands<sup>4</sup>

Good barriers make good languages. Scholars have long speculated that geographical barriers impede linguistic contact between speech communities, and promote language diversification in a manner similar to allopatric speciation. This hypothesis, however, has seldom been tested systematically and quantitatively. Here I adopt methods from evolutionary biology and attempt to quantify the influence of geographical barriers on the degree of language diversification in the Japanese Islands. Measuring the degree of beta diversity from basic vocabularies, I find that geographical proximity and, more importantly, isolation by surrounding ocean, independently explains a significant proportion of lexical variation across Japonic languages. Further analyses indicate that these results are neither a byproduct of using a distance matrix derived from a false phylogeny nor an epiphenomenon of accelerated evolutionary rates in languages spoken by small communities. The finding I report here is the first quantitative evidence that physical barriers formed by water can influence language diversification, and points to an intriguing common mechanism between linguistic and biological evolution.

<sup>&</sup>lt;sup>4</sup> This chapter is currently under review.

#### **4.1.** Introduction

The Galápagos Islands, a cluster of extinct volcanoes in the Pacific Ocean, display a spectacular biodiversity that inspired the most important of all biological theories, Charles Darwin's theory of evolution by natural selection (Darwin, 1859). Finches, iguanas and giant tortoises in these islands appeared unmistakably different not only from mainland South America but also from one island to the next. One hundred and fifty years later, we are beginning to understand that factors giving rise to the biodiversity in these islands are extremely complex (Grant & Grant, 2011), but we know that one simple and the most powerful factor that accounts for many aspects of this biodiversity is geographical isolation among islands (Losos & Ricklefs, 2009; Parent, Caccone, & Petren, 2008).

The fruits of Darwin's visit to the Galápagos Islands, including his historical insight that species evolve by a process of descent with modification, have benefited many scientific disciplines ever since (Dennett, 1996). In particular, an area that is flourishing with Darwinian thinking is the study of language change and variation (Atkinson & Gray, 2005; Croft, 2009; Levinson & Gray, 2012; Pagel, 2009): high-resolution phylogenies inferred from a selection of conservative lexicons shed light on the evolutionary history of their speakers (Gray et al., 2009; Gray & Atkinson, 2003); a serial founder-effect model reveals a common African origin of modern humans and their languages with a gradual reduction of genetic and phonemic diversity from Africa (Atkinson, 2011); and words that appear more frequently in everyday speech tend to be more conservative in a manner similar to proteins that have a larger impact on fitness tend to be more conservative (Hirsh & Fraser, 2001; Pagel et al., 2007). These parallels between linguistic and biological evolution are striking, but in comparison to biological evolution, our understanding of why linguistic mutations arise, accumulate, and give birth to different languages are far from complete.

In this chapter, I suggest that the same factor responsible for much of the biodiversity in the Galápagos Islands is also responsible for the linguistic diversity in the Japanese Islands: the geographical isolation that impede interaction between speech communities. The hypothesis that spatially isolated languages gradually diverge from one another due to reduction of linguistic contact has been proposed on theoretical (Sereno, 1991) and anecdotal (Mufwene, 2008) grounds, but the lack of suitable methods and data meant that its validity could not be tested rigorously. A previous investigation on Micronesian languages reported a general trend that distant speech communities tend to speak different languages (Cavalli-Sforza & Wang, 1986), but because it lacked comparable language samples from non-islands, it was impossible to tease apart the influence of geographical isolation from a simple distance decay of linguistic similarity (Nekola & White, 1999; Nettle & Harriss, 2003). Another study using more sophisticated methods (Gray et al., 2010) compared tree-likeness scores of Polynesian languages with those from Indo-European, and found no support for the effect of geographical isolation. This result, however, was difficult to interpret because Indo-European language family is almost three times older than Polynesian, and thus the difference between their evolutionary patterns could potentially be attributed to the difference in their time depth.

Japonic language family provides an ideal testing ground to investigate the influence of geographical isolation on languages diversification for two reasons. First, Japonic languages are distributed across islands of different sizes that naturally allow them to be either separated or connected by geography, thereby forming two naturally comparable conditions (figure 4.1). Secondly, as all extant Japonic variants share a recent common ancestor (Lee & Hasegawa, 2011), the time of their origin is reasonably well controlled and it is thus possible to interpret the influence of geographical barriers in a straightforward manner. Furthermore, a recent genome-wide SNP analysis revealed the structure of

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Japanese population (Yamaguchi-Kabata et al., 2008) at a resolution high enough to be directly compared with linguistic structure, and as previous studies on cultural diversity have shown (Bell, Richerson, & McElreath, 2009; Ross, Greenhill, & Atkinson, 2013; Rzeszutek, Savage, & Brown, 2012), such a comparison provides an invaluable opportunity to uncover the intertwined history of biological and linguistic evolution.



Figure 4.1 Map of 57 Japonic languages. The Japanese Islands comprise 6852 islands of which 258 are inhabited.

#### 4.2. Materials and methods

For the analyses, I defined linguistic diversity as beta diversity (Anderson, Ellingsen, & McArdle, 2006) of lexicons, which is expressed as dissimilarity among basic vocabularies of language variants for a given area, measured by patristic or Jaccard distances. Patristic distance is defined as the total branch length connecting two taxa on a tree, and the patristic distances were extracted from Bayesian inference of Japonic language phylogeny (Lee & Hasegawa, 2011), using an R package *ape* (Paradis, Claude, & Strimmer, 2004; R Core Team, 2013). The Jaccard distance quantifies the degree of dissimilarity between a pair of variants by estimating the number of dissimilar traits between them, normalized by the total number of their traits. The Jaccard distances were calculated from binary states indicating presence ('1') or absence ('0') of a cognate (Crowley & Bowern, 2009) among Japonic variants (Lee & Hasegawa, 2011), using an R package vegan (Oksanen et al., 2013). The Jaccard distance is often considered as an appropriate measure of cultural diversity because it disregards shared absence of traits and normalizes the distance for each pair (Rogers & Ehrlich, 2008; Ross et al., 2013). I computed the Jaccard distances in order to address a potential criticism that the patristic distances are inappropriate estimates derived from a false phylogeny.

I used binary states to indicate presence ('1') or absence ('0') of isolation by ocean between any two variants in a matching matrix. The current coding scheme is conservative in that presence of ocean separating any two variants was coded as 1 regardless of the distance between them. This may be meaningless for some speech communities in Ryukyu Islands of southern Japan who developed advanced sailing technology and complex trade networks with neighbouring countries from early times (Smits, 1999). I expect, however, that the conservative coding scheme used here is likely to underestimate the effects of geographical

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isolation rather than overestimate them. Pairwise geographical proximity among Japonic variants were obtained by calculating great circle distances from their geographic coordinates, using GenAIEx v.6.5 (Peakall & Smouse, 2012). The geographical coordinates of Japonic variants were the centroids of the locations from which the variants were sampled (Hirayama, 1988; 1992).

The extent of pairwise correlations between geographical proximity, isolation by surrounding water, and patristic/Jaccard distance matrices was determined by using the Mantel and partial Mantel tests (Mantel, 1967; Smouse, Long, & Sokal, 1986). The Mantel test calculates a correlation between two dissimilarity matrices, and partial Mantel test calculates a partial correlation between two matrices while controlling for a third matrix. Because the elements of a distance matrix are not independent, statistical significance of the Mantel and partial Mantel tests are determined by permutation testing, and the estimates were obtained from 9999 permutations for each test (Oksanen et al., 2013). In addition to the standard Pearson product-moment correlation coefficient, I also estimated a rank correlation coefficient using Kendall's tau to examine the robustness of results.

I used NeighborNet algorithm (Huson & Bryant, 2006) to visualize the relationships among Japonic variants. For this, I used gene-content distances (Gray et al., 2010) and plotted split graphs while filtering out splits below a threshold of 0.001. I then estimated their tree-likeness with the delta (Holland et al., 2002) and *q*-residual scores (Gray et al., 2010). Split graphs and their tree-likeness scores can measure the extent of conflicting signal within a dataset, and the conflicting signal indicates hybridization, horizontal transfer, and convergent evolution.

In order to explore the relationship between genetic and linguistic structures, I used Arlequin v.3.5.1.3 (Excoffier & Lischer, 2010) to calculate  $\Phi_{ST}$  from

patristic/Jaccard distance matrices, and compared them with  $F_{ST}$  obtained from a previous genome-wide SNP analysis involving 7003 individuals (Yamaguchi-Kabata et al., 2008). Linguistic subpopulations were defined in the same scheme as the genetic subpopulations [i.e., Hokkaido, Tohoku, Kanto-Koshinetsu, Tokai-Hokuriku, Kinki, Kyushu, and Okinawa; see figure 1 of (Yamaguchi-Kabata et al., 2008)]. In general,  $\Phi_{ST}$  is considered slightly more informative than  $F_{ST}$  because  $\Phi_{ST}$  takes into account distance differences among variants. In essence, however, they are similar in that both measure the proportion of variation among subpopulations in relation to the total variation, and therefore, it is possible to compare  $\Phi_{ST}$  and  $F_{ST}$  directly. I interpreted any negative  $\Phi_{ST}$  value as zero, and used permutation testing to assess statistical significance of the relationship between genetic and linguistic structures.

#### 4.3. Results

Consistent with the hypothesis that geographical barriers promote language diversification in a manner similar to allopatric speciation, the results from simple Mantel tests indicate that pairs of Japonic variants that are separated by ocean tend to be more different from each other than those that are connected by land routes, for both Jaccard (Pearson's correlation r = 0.58, p < 0.001; Kendall's Tau  $r_{\tau} = 0.49$ , p < 0.001) and patristic distances (r = 0.51, p < 0.001;  $r_{\tau} = 0.42$ , p < 0.001). Also, pairs of variants that are geographically distant from each other tend to be more different than those that are close to each other, for both Jaccard (r = 0.78, p < 0.001;  $r_{\tau} = 0.55$ , p < 0.001) and patristic distances (r = 0.76, p < 0.001;  $r_{\tau} = 0.56$ , p < 0.001;  $r_{\tau} = 0.55$ , p < 0.001) and patristic distances (r = 0.76, p < 0.001;  $r_{\tau} = 0.56$ , p < 0.001). In general, geographical proximity explains larger amount of linguistic variability than isolation by surrounding water (table 4.1), and this may be related to Honshu having a linguistic gradient across 1300 kilometres of land without being separated by water. Partial Mantel tests show that the effect of geographical barriers remains meaningful even after geographical proximity is

factored out [Jaccard distances (r = 0.30, p < 0.001;  $r_{\tau} = 0.31, p < 0.001$ ); patristic distances (r = 0.18, p = 0.013;  $r_{\tau} = 0.21, p = 0.002$ )]. I therefore infer that the effect of barriers formed by surrounding water is neither a byproduct of geographical proximity nor a statistical artefact derived from a false phylogeny (table 4.1).

Measure of lexical diversity	Explained by	While controlling for	Estimated by	Variance explained (%)	<i>p</i> -value
Jaccard	Isolation	-	Pearson	22.86	< 0.001
Jaccard	130141011		i carson	33.00	< 0.001
Jaccard	Isolation	-	Kendall	23.82	< 0.001
Patristic	Isolation	-	Pearson	26.25	< 0.001
Patristic	Isolation	-	Kendall	17.37	< 0.001
Jaccard	Proximity	-	Pearson	60.92	< 0.001
Jaccard	Proximity	-	Kendall	30.56	< 0.001
Patristic	Proximity	-	Pearson	57.90	< 0.001
Patristic	Proximity	-	Kendall	31.46	< 0.001
Jaccard	Isolation	Proximity	Pearson	9.13	< 0.001
Jaccard	Isolation	Proximity	Kendall	9.78	< 0.001
Patristic	Isolation	Proximity	Pearson	3.35	0.013
Patristic	Isolation	Proximity	Kendall	4.50	0.002
Jaccard	Proximity	Isolation	Pearson	46.29	< 0.001
Jaccard	Proximity	Isolation	Kendall	17.76	< 0.001
Patristic	Proximity	Isolation	Pearson	44.82	< 0.001
Patristic	Proximity	Isolation	Kendall	20.78	< 0.001

## Table 4.1 Results of the Mantel and partial Mantel tests.

A potential problem with any correlational study is a hidden variable that is linked to the variables of interest (Roberts & Winters, 2013). I thus carried out further analyses to investigate if there is a confounding factor behind the effect of geographical barriers. On closer inspection of the data, I observed that the majority of signal for the current result comes from small isolated islands (i.e., Hachijyo, Amami, Okinawa, Hirara, Ikema, Irafu, Tarama, Taketomi, Ishigaki, Hateruma, and Yonaguni). Considering that smaller communities tend to have higher rates of language evolution as innovations and borrowings spread more easily than in larger communities (Nettle, 1999), one could argue that the current results may be an epiphenomenon of accelerated evolutionary rates in small speech communities. It is difficult to directly test for the effect of population size on language diversification within the Mantel test framework because (i) the exact number of speakers for each Japonic variant is unknown, and (ii) creating a dissimilarity matrix of population size leads to loss of information about which variant has large or small population size. Therefore, I took a different approach by extracting mean evolutionary rates for all variants from Japonic language tree (Lee & Hasegawa, 2011) using TreeStat (Drummond et al., 2012), and tested if the languages from small islands have higher rates of evolution than the rest (table 4.2). The Wilcoxon rank-sum test, however, gave no evidence against the null hypothesis of identical distributions for their evolutionary rates (W = 228, p =0.70; one-sided), suggesting that accelerated evolutionary rates associated with small speech communities may have little influence on the current results.

## Table 4.2 Evolutionary rates extracted from 9000 Japonic language phylogenies.

Numbers indicate the average replacement rates of cognates per year.

Variants	Rates (per year)		
Aichi	0.000364999		
Akita	0.000332053		
Amami	0.000546476		
Aomori	0.000510076		
Chiba	0.00050561		
Ehime	0.000499109		
Fukui	0.000532512		
Fukuoka	0.000615202		
Fukushima	0.000524927		
Gifu	0.000560397		
Gunma	0.000502224		
Hachijyo	0.0004531		
Hateruma	0.000499179		
Hirara	0.000506281		
Hiroshima	0.000512288		
Hokkaido	0.000545269		
Hyogo	0.000529859		
Ibaraki	0.000555217		
Ikema	0.000531185		
Irafu	0.000536667		
Ishigaki	0.000507913		
Ishikawa	0.000510662		
Iwate	0.000493221		
Kagawa	0.000497149		
Kagoshima	0.000503503		
Kanagawa	0.00049827		
Kochi	0.000525414		
Kumamoto	0.000533549		
Kyoto	0.000546553		
Mie	0.000533932		
Miyagi	0.000538337		
Miyazaki	0.00052908		

Nagano	0.000527843
Nagasaki	0.000544378
Nara	0.000529374
Nigata	0.000535208
Oita	0.000540429
Okayama	0.000529802
Okinawa	0.000525457
Osaka	0.000498159
Saga	0.000478517
Saitama	0.00045075
Shiga	0.00047249
Shimane	0.000447209
Shizuoka	0.000410269
Taketomi	0.000455271
Tarama	0.000281373
Tochigi	0.000427384
Tokushima	0.000377302
Tokyo	0.000440558
Tottori	0.000470355
Toyama	0.000491564
Wakayama	0.000436448
Yamagata	0.000439704
Yamaguchi	0.000580167
Yamanashi	0.000392124
Yonaguni	0.000358076

Split graphs showing the results of NeighborNet analyses provide further support for the conclusion made here. Figure 4.2 shows split graphs of two major subgroups of Japonic language family: Ryukyuan group that consists of geographically isolated variants, and mainland Japanese group that consists mostly of variants connected by land routes. Clearly, the split graph of mainland Japanese on the left side shows a strong conflicting signal than that of Ryukyuan on the right. Furthermore, when I quantify the amount of conflicting signal for each group, mainland Japanese shows the average delta score of 0.394 and q-residual score of 0.02, and Ryukyuan shows the delta score = 0.23 and *q*-residual = 0.004. As smaller numbers indicate less conflicting signal, these estimates suggest that, in comparison to Ryukyuan, mainland Japanese carries a stronger signature of hybridization, horizontal transfer, and convergent evolution. If I make a crude generalization that these two subgroups roughly represent the presence/absence of isolation by surrounding water, then since (i) Ryukyuan variants and mainland Japanese variants have similar time depth as all Japonic variants are descendants of a 2200-year-old common ancestor, (ii) there is no detectable difference in their evolutionary rates (W = 245, p = 0.84), and (iii) mainland Japanese variants seem to have experienced more intense linguistic contact than Ryukyuan variants, I can infer that the island geography as well as impediment of linguistic contact must be the main factors driving linguistic diversity in the Japanese Islands.



Figure 4.2 Split graphs showing the results of NeighborNet analyses on mainland Japanese (left) and Ryukyuan (right). Gene-content distances were used and splits were filtered to a threshold of 0.001. Subgroups of Japonic languages are coded with colour circles: red-Hachijyo; orange-western Japanese; yellow-eastern Japanese; blue-Kyushu; purplenorthern Ryukyuan; pink-southern Ryukyuan. Reticulations indicate presence of conflicting signal, which can be interpreted as hybridization, horizontal transfer, and convergent evolution. Scale bar: 0.01.

Comparing the structures between genetic and linguistic variation reveals that the patterns of their internal population differentiation are strongly correlated [patristic distance (r = 0.79, p = 0.03;  $r_{\tau} = 0.52$ , p = 0.04); Jaccard distance (r = 0.75, p= 0.05;  $r_{\tau}$  = 0.46, p = 0.05); simple mantel tests with 9999 permutations]. This implies that if genetic variation of a particular subgroup is highly differentiated from the rest, then linguistic variation of the same subgroup is also highly differentiated from the rest, or vice versa. Moreover, it seems unlikely that the similarity between the two structures is a consequence of sharing geographical proximity [patristic distance (r = 0.75, p = 0.03;  $r_{\tau} = 0.48$ , p = 0.04); Jaccard distance  $(r = 0.66, p = 0.08; r_{\tau} = 0.34, p = 0.08)$ ; partial mantel tests with 9999 permutations; note that  $\Phi_{ST}$  matrix computed from the Jaccard distances fails to show significance at 5% level, but because the data points are too small ( $7 \times 7$  matrix) to generate a proper null distribution and the p-values are reasonably low, I interpret these estimates to be generally meaningful; table 4.3]. Overall, these estimates seem to suggest that the evolution of both systems has experienced similar historical factors that are relevant to the Japanese Islands, and support the idea that human genes and languages often evolve by a shared process of descent with modification. Intriguingly, the range of pairwise linguistic  $\Phi_{\rm ST}$  values (0.0562 – (0.8903) is orders of magnitude higher than that of genetic  $F_{ST}$  values ((0.0002 -0.0035). Such a pattern has been argued to be a residual of cultural selection (Bell et al., 2009), and if correct, it is possible to hypothesize that further clues to the forces driving language diversification in the Japanese Islands may be found in culture, rather than genes, such as political dominance by regional speech communities (Hock, 1986; Renfrew, 1989) or social networks moderated by shared linguistic markers (McElreath, Boyd, & Richerson, 2003; Nettle & Dunbar, 1997).
#### Table 4.3 Results of analysis of variance on linguistic and genetic data. Upper

triangular matrix represents the mean  $\Phi_{\rm ST}$  calculated from patrixtic distances and lower triangular matrix represent the mean  $F_{\rm ST}$  obtained from genome-wide SNP analysis.

	Hokkaido	Tohoku	Kanto- Kosinetsu	Tokai- Hokuriku	Kinki	Kyushu	Okinawa
Hokkaido	-	0.81267	0.16985	0.32306	0.66131	0	0.84067
Tohoku	0.000606	-	0.24242	0.36711	0.67301	0.30067	0.89031
Kanto- Kosinetsu	0.000293	0.000414	-	0.09122	0.37172	0.20726	0.86169
Tokai- Hokuriku	0.000636	0.00077	0.000409	-	0.31405	0.15505	0.85763
Kinki	0.000443	0.000642	0.000229	0.000551	-	0.18951	0.87979
Kyushu	0.000552	0.000687	0.000322	0.000659	0.000435	-	0.74672
Okinawa	0.003381	0.003282	0.003138	0.003522	0.003452	0.002823	-

### 4.4. Discussion

Languages grow and diversify across different landscapes. The preliminary results presented here suggest that geographical isolation of many Japanese islands may have impeded hybridization and/or horizontal transfer among speech communities, and promoted language diversification in Japonic language family. A series of tests shows that the current results are unlikely to be a byproduct of (i) using a false language phylogeny, (ii) a simple distance decay of similarity, and (iii) accelerated language evolution of small speech communities. Based on these observations, I further suggest that our current understanding of linguistic diversity will be greatly improved if we take into account the same factor that led Darwin to his historical discovery: the geographical isolation among islands (Darwin, 1859; Losos & Ricklefs, 2009; Parent et al., 2008).

At the same time, I acknowledge that the analogy breaks down when it is considered that, unlike many species of the Galápagos Islands, the people of the Japanese Islands had advanced sailing skills which may have allowed them to migrate from one island to another at will (Hudson, 1999; Smits, 1999). Therefore, although I argue that geographical barriers among the Japanese Islands played a significant role in driving linguistic diversity, I expect that there must also be other contributing factors that maintained the diversity until present.

I suggest that further clues to the process of language diversification in the Japanese Islands can be gained from the comparison between genetic and linguistic population structures. The results indicate that (i) the degrees of pairwise population differentiation between the two structures are highly correlated, indicating that similar evolutionary forces have shaped both genetic and linguistic diversity, and (ii) linguistic  $\Phi_{ST}$  values are on average much higher than the corresponding genetic  $F_{ST}$  values, suggesting that cultural factors had

more influence on the development of population structure than genetic factors (Bell et al., 2009). If correct, two different but related scenarios can be formulated. The first scenario is a bottom-up process: once sufficient linguistic diversity arose to the point that speech communities could reliably distinguish one variant from another, linguistic dissimilarity may have been further amplified and maintained by being adopted as a marker for detecting as well as signalling one's membership in reciprocal exchange network (Nettle & Dunbar, 1997) or one's behavioural type in social interactions (McElreath et al., 2003), which subsequently led to the developments of stable regional clusters of social groups that shaped genetic and linguistic diversity. Perhaps the use of social markers may have been easier in small isolated communities than in sizeable communities (Boyd & Richerson, 1988), which coincides with the observation that the signal for the current results comes mainly from small isolated islands.

The second scenario is a top-down process: when proto-Japonic speakers arrived in the Japanese Islands around 2,500 years ago, they were divided into several small-scale competing groups (Lee & Hasegawa, 2011), and political unification for mainland Japanese was achieved only around 1,200 years ago, followed by the unification for isolated islands of Ryukyu around 500 years ago (Hudson, 1999). Therefore, the correlated but linguistically more accentuated population structures could be simply reflecting the accumulated effects of territorial barriers imposed by regional hereditary clans (Hock, 1986; Renfrew, 1989) which might have coincided with the natural barriers such as surrounding ocean. The scenarios described here are speculative and should be subjected to further research, but they illustrate how evidence from different lines of inquiry can be synthesized to build a consistent model of human diversity.

The current study makes a contribution to the current state of research on language evolution by demonstrating that there is an alternative way of measuring

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linguistic diversity, which is beta diversity of lexicons. Previous studies have placed disproportionate emphasis on Greenberg's diversity index (i.e., the probability of two randomly chosen speakers sharing the same language) or language density over a given area or per population (Gavin et al., 2013). While they are scientifically sound methods, they potentially suffer from problematic nature of how languages are defined [see (Nettle, 1998) for conceptual review]. I argue that if (i) language variants are sampled evenly across a region, and (ii) there is a sufficient amount of variation among them, then measuring beta diversity may serve as an excellent complementary strategy for revealing the external factors that shape language diversity (Koleff, Gaston, & Lennon, 2003; Nettle et al., 2007).

A major limitation to this study is the lack of more ecologically sensitive measure for detecting geographical barriers. I focused on separation by ocean as the sole mechanism for geographical isolation, but it is obvious that numerous mountains of Honshu must have been significant barriers preventing some speech communities from interacting with one another. A previous study that examined the frequencies of 15 genetic markers in Japanese population reported that some of the montane regions of Honshu may have indeed contributed to rapid genetic change (Sokal & Thomson, 1998). Although this information was not incorporated into the current analyses because the identified montane regions were incompatible with the required level of resolution, the search for other plausible ecological barriers is a direction that deserves more attention. In addition, the coding scheme used here may also be improved by assigning different weights to different barriers based on seasonal wind change or the direction of water circulation (Jin, Wang, Liu, & Zhang, 2010; Moon, Hirose, Yoon, & Pang, 2009) as they would have determined the difficulty of sea travel. The findings presented here are mainly correlational and therefore preclude causal interpretation. While I agree that interpretations from correlations should be made carefully, I believe that the methods and data used in this study are ideally suited for the phenomenon of interest, and the current approach opens the possibility for further characterization of this fascinating phenomenon. We still have a long way to go to fully understand the dynamics of language diversification. Nevertheless, the results presented here demonstrate how relatively simple procedures can start revealing linguistic consequences of geographical isolation, and illustrate how genes and languages evolve by a common process of descent with modification.

## **Chapter Five**

## Conclusion

Just as the great Tree of Life grows on the surface of Earth, the Tree of Language grows on the collective minds of our species. Close inspection into the history discloses that the idea of languages forming an independent category of evolution is neither new nor naïve. Rudimentary forms of the idea can be found almost the same time as Charles Darwin put forth his theory of evolution (Schleicher, 1869), and through trial and error, language evolution gradually grew from a humble speculation to a legitimate subject of science in the last few millennia (Atkinson & Gray, 2005). While there also exist numerous differences, the evolutionary pattern and process between life and language are curiously connected.

The chapters described in this thesis show us that, as we untangle the complex branches of language tree and explore the forest of language evolution back in time, the tales of how languages evolved and perished are in fact tales about ourselves: how we expanded into different landscapes at certain times in history, and how it in return shaped the evolution of ourselves and our languages. In Chapter 2 and 3, I analysed a set of lexicons that are known to preserve historical signal, and reconstructed evolutionary patterns of the Ainu and Japonic languages in space and time. The estimates from the two language groups indicated that their origins are deeply related to particular prehistoric events of human migration. More specifically, in Chapter 2, the prehistoric pattern of how Ainu language arose and spread was described, and the results were in agreement with a theory that the Okhotsk migration played a major role in shaping biology and culture of the Ainu. This challenges the prevailing dual structure model of the Ainu origin, and reopens the debate that once thought to have been settled. From the reconstructed pattern, I was able to not only shed light on the evolutionary force shaping the linguistic diversity of the Ainu but also formulate a new testable hypothesis that the transmission of the Ainu language may have been genderspecific. This hypothesis is yet to be tested as such an investigation requires more cultural and genetic data, but the stream of reasoning that led to this hypothesis demonstrates how the framework of pattern and process provides an effective way for making progress in understanding the evolution of languages as well as their speakers.

Chapter 3 described the results from analysing linguistic diversity of Japonic language family and its root age. The estimates were consistent with a hypothesis that Japonic languages originated from an ancient language spoken by prehistoric farmers who expanded into the Japanese Islands around 2,500 years ago. One of the main purposes of Chapter 3 was to examine the validity of these conclusions through discussing several criticisms raised by scholars of different disciplines. Although the findings presented in this chapter are unlikely to be the final word on the evolutionary history of Japonic languages, I strongly believe that the justification and validation shown in this chapter provide more than enough confidence for retaining the initial conclusions. A benefit of discussing the criticisms regarding the pattern of Japonic languages was the discovery of a hitherto untested hypothesis about a potential process underlying Japonic language evolution.

More specifically, in attempt to explain why node supports are noticeably lower among mainland Japanese variants than among Ryukyuan variants, it was hypothesized that a particular feature of geography might have shaped linguistic diversity in the Japanese Islands, namely the physical isolation among speech communities. Accordingly, Chapter 4 adopted correlational techniques from

evolutionary biology, and examined if geographical isolation could indeed explain meaningful amount of linguistic diversity (as measured by lexical dissimilarity among Japonic language variants). The results provided support for a hypothesis that geographical isolation leads to language diversification by interfering linguistic contact among speech communities on islands. In addition, I compared results from the analysis of variance on genetic and linguistic structures in the Japanese Islands, and put forth two different but related evolutionary processes that might guide further investigation into the evolutionary process behind language diversification.

As remarked several times throughout the thesis, the study of language evolution, as a whole, has just stepped into the forest of languages and learnt about a few things from a handful number of trees on its outskirts. It is not difficult to imagine that the forest is large, and the path will only get more challenging as we go deeper into it. One of the major challenges that the field of language evolution should overcome in the future is the time barrier. Unlike molecular evolution, the search for language roots is recoverable only up to a certain point in time of history, due to rapid loss of historical signal among languages (Gray, 2005). Some scholars suggest that structural properties such as sound systems or grammar evolve at much slower rates, and thus they may constitute a suitable dataset to reveal deep relationships between languages (Dunn et al., 2005; 2008). Also, other scholars suggest that highly selective ultraconserved words might also be suitable for studying deep history (Pagel, Atkinson, Calude, & Meade, 2013b). Unfortunately, the benefits of using structural features or ultraconserved words are still debated (Greenhill, Drummond, & Gray, 2010b; Pagel, Atkinson, Calude, & Meade, 2013a), and thus the challenge remains to be elucidated in the future.

The other major challenge the field should address in the future is its reliance on linguistic scholarship for identifying and reconstructing cognates. Almost all

language data that are currently being used in literature are processed manually by the comparative method, and the procedure is extremely time consuming and requires painstaking labour. As a result, the language data available for analysis is typically limited to those datasets that have already been worked out by linguists. Ideally, the field of language evolution would benefit if there were a way to automatize this procedure in a manner similar to biologists automatize the sequencing and alignment procedure. While some scholars are starting to make methodological innovations to resolve this issue (Bouchard-Côté, Hall, Griffiths, & Klein, 2013; Kondrak & Sherif, 2006), the accuracy of these methods still falls somewhat short of the reliability of manual process. Nevertheless, it seems only a matter of time that these methods will one day be mature enough to replace human labour and automatize the entire procedure, and one day we may be able to freely explore hitherto unexamined languages from every corner of the globe by outsourcing this process to computer algorithms.

Although small in numbers, the chapters in this thesis are examples of how the framework of pattern and process can be put into practice: the observed regularity of nature (i.e., spatiotemporal patterns of the Ainu and Japonic languages) provides direct clues about the forces that shaped their diversity (i.e., population expansions), and from the results from Japonic language phylogeny a hypothesis was formulated and tested (i.e., the case of geographical isolation promoting language divergence). Also, through triangulation of different lines of evidence, more testable process hypotheses were proposed such as the hypothetical sex-specific transmission of the Ainu language (Chapter 2) or the hypothetical cultural factors contributing to population structure among Japonic speakers (Chapter 4). If these hypothesized processes are correct, then their evolutionary signatures might be observable in the patterns of variation among certain linguistic properties.

We still have a long way to go, but if we continue marching to the beat of pattern and process, along with principled research protocols as well as sophisticated statistical methods, future studies will make even more astonishing and unexpected discoveries, and take us deeper and deeper into the mysterious forest of languages.

# References

- Adachi, N., Shinoda, K., Umetsu, K., Kitano, T., Matsumura, H., Fujiyama, R., et al. (2011). Mitochondrial DNA analysis of Hokkaido Jomon skeletons: remnants of archaic maternal lineages at the southwestern edge of former Beringia. *American Journal of Physical Anthropology*, 146(3), 346–360. doi:10.1002/ajpa.21561
- Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & F. Csaki (Eds.), (Vol. 1, pp. 267–281).
  Presented at the Second International Symposium on Information Theory, Budapest (Hungary): Akademia Kiado.
- Alekseyenko, A. V., Lee, C. J., & Suchard, M. A. (2008). Wagner and Dollo: a stochastic duet by composing two parsimonious solos. *Systematic Biology*, 57(5), 772–784. doi:10.1080/10635150802434394
- Anderson, M. J., Ellingsen, K. E., & McArdle, B. H. (2006). Multivariate dispersion as a measure of beta diversity. *Ecology Letters*, 9(6), 683–693. doi:10.1111/j.1461-0248.2006.00926.x
- Atkinson, Q. D. (2011). Phonemic diversity supports a serial founder effect model of language expansion from Africa. *Science*, *332*(6027), 346–349.
  doi:10.1126/science.1199295
- Atkinson, Q. D., & Gray, R. D. (2005). Curious parallels and curious connections--phylogenetic thinking in biology and historical linguistics. *Systematic Biology*, 54(4), 513–526. doi:10.1080/10635150590950317

- Atkinson, Q. D., & Gray, R. D. (2006). How old is the Indo-European language family? Illumination or more moths to the flame. *Phylogenetic Methods and the Prehistory of Languages. Cambridge: the McDonald Institute for Archaelogical Research*, 91–109.
- Atkinson, Q. D., Meade, A., Venditti, C., Greenhill, S. J., & Pagel, M. (2008). Languages evolve in punctuational bursts. *Science*, *319*(5863), 588–588. doi:10.1126/science.1149683
- Baele, G., Lemey, P., Bedford, T., Rambaut, A., Suchard, M. A., & Alekseyenko,
  A. V. (2012). Improving the accuracy of demographic and molecular clock
  model comparison while accommodating phylogenetic uncertainty. *Molecular Biology and Evolution*. doi:10.1093/molbev/mss084
- Bell, A. V., Richerson, P. J., & McElreath, R. (2009). Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences of the United States of America*, 106(42), 17671–17674. doi:10.1073/pnas.0903232106
- Bellwood, P. S. (2005). *The first farmers: origins of agricultural societies*. Malden, MA: Blackwell Pub.
- Bergsland, K., & Vogt, H. (2010). On the validity of glottochronology. *Current Anthropology*, 3(2), 1–40. doi:10.1086/200264
- Bielejec, F., Rambaut, A., Suchard, M. A., & Lemey, P. (2011). SPREAD: spatial phylogenetic reconstruction of evolutionary dynamics. *Bioinformatics*, 27(20), 2910–2912. doi:10.1093/bioinformatics/btr481
- Blust, R. (2000). Why lexicostatistics doesn't work: the 'universal constant' hypothesis and the Austronesian languages. In C. Renfrew, A. McMahon, & L. Trask (Eds.), *Time depth in historical linguistics* (Vol. 2, pp. 311–332).
  Cambridge: McDonald Institute for Archaeological Research.

- Bouchard-Côté, A., Hall, D., Griffiths, T. L., & Klein, D. (2013). Automated reconstruction of ancient languages using probabilistic models of sound change. *Proceedings of the National Academy of Sciences of the United States of America*, 1–36. doi:10.1073/pnas.1204678110
- Bouckaert, R., Lemey, P., Dunn, M., Greenhill, S. J., Alekseyenko, A. V., Drummond, A. J., et al. (2012). Mapping the origins and expansion of the Indo-European language family. *Science*, *337*(6097), 957–960. doi:10.1126/science.1219669
- Bowern, C., Epps, P., Gray, R. D., Hill, J., Hunley, K., McConvell, P., & Zentz, J.
  (2011). Does lateral transmission obscure inheritance in hunter-gatherer
  languages? *PLOS ONE*, 6(9), e25195. doi:10.1371/journal.pone.0025195.too1
- Box, G. E. P., & Draper, N. R. (1987). *Empirical model-building and response surfaces*. Oxford: John Wiley & Sons Inc.
- Boyd, R., & Richerson, P. J. (1988). The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology*, 132(3), 337–356. doi:10.1016/S0022-5193(88)80219-4
- Cavalli-Sforza, L. L., & Wang, W. S.-Y. (1986). Spatial distance and lexical replacement. *Language*, 38–55.
- Cavalli-Sforza, L. L., Piazza, A., Menozzi, P., & Mountain, J. (1988). Reconstruction of human evolution: bringing together genetic, archaeological, and linguistic data. *Proceedings of the National Academy of Sciences*, 85(16), 6002– 6006. doi:10.1073/pnas.85.16.6002
- Clarke, H. (1989). The development of Edo language. In C. A. Gerstle (Ed.), *18th century Japan: culture and society* (pp. 63–72). Richmond: Curzon Press.
- Croft, W. (2009). Evolutionary Linguistics. *Annual Review of Anthropology*, 37(1), 219–234. doi:10.1146/annurev.anthro.37.081407.085156

- Crowley, T., & Bowern, C. (2009). *An introduction to historical linguistics*. Oxford, London: Oxford University Press.
- Currie, T. E., Greenhill, S. J., Gray, R. D., Hasegawa, T., & Mace, R. (2010). Rise and fall of political complexity in island South-East Asia and the Pacific. *Nature*, 467(7317), 801–804. doi:10.1038/nature09461
- Darwin, C. (1859). On the origin of species. London: Murray.
- Darwin, C. (1871). The descent of man. London: Murray.
- Dediu, D., & Levinson, S. C. (2012). Abstract profiles of structural stability point to universal tendencies, family-specific factors, and ancient connections between languages. *PLOS ONE*, 7(9), e45198.
  doi:10.1371/journal.pone.0045198.too2
- Dennett, D. C. (1996). Darwin's dangerous idea. New York: Simon and Schuster.
- Diamond, J., & Bellwood, P. (2003). Farmers and their languages: the first expansions. *Science*, 300(5619), 597–603. doi:10.1126/science.1078208
- Dodo, Y., & Kawakubo, Y. (2002). Cranial affinities of the epi-Jomon inhabitants in Hokkaido, Japan. *Anthropological Science*, 110(1), 1-32. doi:10.1537/ase.110.1
- Drummond, A. J., Ho, S. Y. W., Phillips, M. J., & Rambaut, A. (2006). Relaxed phylogenetics and dating with confidence. *PLOS Biology*, 4(5), e88. doi:10.1371/journal.pbio.0040088.sdoo1
- Drummond, A. J., Rambaut, A., Shapiro, B., & Pybus, O. G. (2005). Bayesian coalescent inference of past population dynamics from molecular sequences.
   *Molecular Biology and Evolution*, 22(5), 1185–1192. doi:10.1093/molbev/msi103

- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 1-4. doi:10.1093/molbev/mss075
- Dunn, M., Levinson, S. C., Lindström, E., Reesink, G., & Terrill, A. (2008).
  Structural phylogeny in historical linguistics: methodological explorations applied in Island Melanesia. *Language*, 84(4), 710–759. doi:10.1353/lan.0.0069
- Dunn, M., Terrill, A., Reesink, G., Foley, R. A., & Levinson, S. C. (2005).
   Structural phylogenetics and the reconstruction of ancient language history. *Science*, 309(5743), 2072–2075. doi:10.1126/science.1114615

Embleton, S. M. (1986). Statistics in historical linguistics. Bochum: Brockmeyer.

Excoffier, L., & Lischer, H. E. L. (2010). Arlequin suite ver 3.5: a new series of programs to perform population genetics analyses under Linux and Windows.
 Molecular Ecology Resources, 10(3), 564–567. doi:10.1111/j.1755-0998.2010.02847.x

Felenstein, J. (2004). Inferring phylogenies. Sunderland: Sinauer Associates.

- Fitch, W. M., & Ayala, F. J. (1994). Tempo and mode in evolution. *Proceedings of the National Academy of Sciences*, 91(15), 6717–6720.
- Forster, P., & Renfrew, C. (2011). Mother tongue and Y chromosomes. *Science*, *333*(6048), 1390–1391. doi:10.1126/science.1205331
- Frellesvig, B., & Whitman, J. (Eds.). (2008). *Proto-Japanese: issues and prospects* (Vol. 294). Chicago: John Benjamins Publishing.
- Garrett, A. (2006). Phylogenetic methods and the prehistory of languages. In P.
  Forster & C. Renfrew (Eds.), *Phylogenetic methods and the prehistory of languages* (pp. 139–151). Cambridge: McDonald Institute for Archaeological Research.

- Gavin, M. C., Botero, C. A., Bowern, C., Colwell, R. K., Dunn, M., Dunn, R. R., et al. (2013). Toward a mechanistic understanding of linguistic diversity. *BioScience*, 63(7), 524–535. doi:10.1525/bio.2013.63.7.6
- Gelman, A., & Meng, X.-L. (1998). Simulating normalizing constants: From importance sampling to bridge sampling to path sampling. *Statistical Science*, 163–185.
- Grant, P. R., & Grant, B. R. (2011). *How and why species multiply*. New Jersey: Princeton University Press.
- Gray, R. D. (2005). Pushing the time barrier in the quest for language roots. Science, 309(5743), 2007–2008. doi:10.1126/science.1114383)
- Gray, R. D., & Atkinson, Q. D. (2003). Language-tree divergence times support the Anatolian theory of Indo-European origin. *Nature*, 426(6965), 435–439. doi:10.1038/nature02029
- Gray, R. D., & Jordan, F. M. (2000). Language trees support the express-train sequence of Austronesian expansion. *Nature*, 405(6790), 1052–1055. doi:10.1038/35016575
- Gray, R. D., Bryant, D., & Greenhill, S. J. (2010). On the shape and fabric of human history. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 365(1559), 3923–3933. doi:10.1073/pnas.93.4.1381
- Gray, R. D., Drummond, A. J., & Greenhill, S. J. (2009). Language phylogenies reveal expansion pulses and pauses in Pacific settlement. *Science*, 323(5913), 479–483. doi:10.1126/science.1166858
- Gray, R. D., Greenhill, S. J., & Ross, R. M. (2007). The pleasures and perils of Darwinizing culture (with phylogenies). *Biological Theory*, 2(4), 360–375. doi:10.1162/biot.2007.2.4.360

- Greenhill, S. J., & Gray, R. D. (2009). Austronesian language phylogenies: myths and misconceptions about Bayesian computational methods. In A. Adelaar & A. Pawley (Eds.), *Austronesian historical linguistics and culture history: a festschrift for Robert Blust* (pp. 1–23). Canberra: Pacific Linguistics.
- Greenhill, S. J., Atkinson, Q. D., Meade, A., & Gray, R. D. (2010a). The shape and tempo of language evolution. *Proceedings of the Royal Society of London B Biological Sciences*, 277(1693), 2443–2450. doi:10.1098/rspb.2010.0051
- Greenhill, S. J., Blust, R., & Gray, R. D. (2008). The Austronesian basic vocabulary database: from bioinformatics to lexomics. *Evolutionary Bioinformatics*, 4, 271.
- Greenhill, S. J., Currie, T. E., & Gray, R. D. (2009). Does horizontal transmission invalidate cultural phylogenies? *Proceedings of the Royal Society of London B Biological Sciences*, 276(1665), 2299–2306. doi:10.1098/rspb.2008.1944
- Greenhill, S. J., Drummond, A. J., & Gray, R. D. (2010b). How accurate and robust are the phylogenetic estimates of Austronesian language relationships? *PLOS ONE*, 5(3), e9573. doi:10.1371/journal.pone.0009573.g003
- Hammer, M. F., Karafet, T. M., Park, H., Omoto, K., Harihara, S., Stoneking, M., & Horai, S. (2006). Dual origins of the Japanese: common ground for hunter-gatherer and farmer Y chromosomes. *Journal of Human Genetics*, 51(1), 47–58. doi:10.1007/s10038-005-0322-0
- Hanihara, K. (1991). Dual structure model for the population history of Japanese. *Japan Review*, 2, 1–33.
- Hanihara, T. (2010). Metric and nonmetric dental variation and the population structure of the Ainu. *American Journal of Human Biology*, 22(2), 163–171. doi:10.1002/ajhb.20969

- Hanihara, T., & Ishida, H. (2009). Regional differences in craniofacial diversity and the population history of Jomon Japan. *American Journal of Physical Anthropology*, 139(3), 311–322. doi:10.1002/ajpa.20985
- Haspelmath, M., & Tadmor, U. (2009). *Loanwords in the world's languages: a comparative handbook*. Berlin: Mouton de Gruyter.
- Hattori, S. (1961). A Glottochronological Study on Three Okinawan Dialects. International Journal of American Linguistics, 27(1), 52–62.
- Hattori, S. (1978-1979). Nihon sogo ni tsuite. Gekkan Gengo, 7-8(1-3, 6-12).
- Hattori, S., & Chiri, M. (1960). A lexicostatistic study on the Ainu dialects. *The Japanese Journal of Ethnology*, 24, 31–66. Retrieved from http://ci.nii.ac.jp/naid/110001838079/en/
- Hempel, C. G., & Oppenheim, P. (1948). Studies in the logic of explanation. *Philosophy of Science*, 15(2), 135–175. doi:10.2307/185169
- Hirayama, T. (1988). Minami Ryukyū no Hogenkisogoi. Tokyo: Ohfusya.
- Hirayama, T. (1992). Gendai Nihongohōgen Daijiten. Tokyo: Meiji Shoin.
- Hirsh, A. E., & Fraser, H. B. (2001). Protein dispensability and rate of evolution. *Nature*, 411(6841), 1046–1049. doi:10.1038/35082561
- Hock, H. H. (1986). Principles of historical linguistics. Berlin: Mouton de Gruyter.
- Hoeting, J. A., Madigan, D., Raftery, A. E., & Volinsky, C. T. (1999). Bayesian model averaging: a tutorial. *Statistical Science*, 382–401. doi:10.2307/2676803
- Holden, C. J. (2002). Bantu language trees reflect the spread of farming across sub-Saharan Africa: a maximum-parsimony analysis. *Proceedings of the Royal Society of London B Biological Sciences*, 269(1493), 793–799. doi:10.1098/rspb.2002.1955

- Holder, M., & Lewis, P. O. (2003). Phylogeny estimation: traditional and Bayesian approaches. *Nature Reviews Genetics*, 4(4), 275–284. doi:10.1038/nrg1044
- Holland, B. R., Huber, K. T., Dress, A., & Moulton, V. (2002). δ plots: A tool for analyzing phylogenetic distance data. *Molecular Biology and Evolution*, 19(12), 2051–2059. doi:10.1093/oxfordjournals.molbev.a004030
- Holt, W. S. (1933). *Treaties defeated by the senate*. Baltimore: The Johns Hopkins Press.
- Hudson, M. (1999). *Ruins of identity: ethnogenesis in the Japanese Islands*. Honolulu: University of Hawaii'i Press.
- Hudson, M. J. (2004). The perverse realities of change: world system incorporation and the Okhotsk culture of Hokkaido. *Journal of Anthropological Archaeology*, 23(3), 290-308. doi:10.1016/j.jaa.2004.05.002
- Huson, D. H., & Bryant, D. (2006). Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution*, 23(2), 254–267. doi:10.1093/molbev/msj030
- Ishida, H., & Kida, M. (1991). An anthropological investigation of the Sakhalin Ainu with special reference to nonmetric cranial traits. *Journal of the Anthropological Society of Nippon*, 99(1), 23–32.
- Ishida, H., Hanihara, T., Kondo, O., & Fukumine, T. (2009). Craniometric divergence history of the Japanese populations. *Anthropological Science*, *117*(3), 147–156. doi:10.1537/ase.081219
- Jeffreys, H. (2008). Some tests of significance, treated by the theory of probability. *Mathematical Proceedings of the Cambridge Philosophical Society*, 31(02), 203–222. doi:10.1017/S030500410001330X

- Jin, B., Wang, G., Liu, Y., & Zhang, R. (2010). Interaction between the East China Sea Kuroshio and the Ryukyu Current as revealed by the selforganizing map. *Journal of Geophysical Research: Oceans (1978–2012)*, *115*(C12). doi:10.1029/2010JC006437
- Jinam, T., Nishida, N., Hirai, M., Kawamura, S., Oota, H., Umetsu, K., et al. (2012). The history of human populations in the Japanese Archipelago inferred from genome-wide SNP data with a special reference to the Ainu and the Ryukyuan populations. *Journal of Human Genetics*, 57(12), 787–795. doi:doi:10.1038/jhg.2012.114
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19(2), 101–108. doi:10.1016/j.tree.2003.10.013
- Jordan, F., Gray, R. D., Greenhill, S. J., & Mace, R. (2009). Matrilocal residence is ancestral in Austronesian societies. *Proceedings of the Royal Society of London B Biological Sciences*, 276(1664), 1957–1964. doi:10.1098/rspb.2009.0088
- Jōdaigo Jiten Henshū Iinkai. (1967). *Jidaibetsu kokugo daijiten. Jōdai hen*. Tokyo: Sanseidō.
- Kass, R. E., & Raftery, A. E. (1995). Bayes factors. Journal of the American Statistical Association, 773–795.
- Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: an experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(31), 10681–10686. doi:10.1073/pnas.0707835105
- Kirch, P. V., & Green, R. C. (2001). *Hawaiki, ancestral polynesia: an essay in historical anthropology*. Cambridge: Cambridge University Press.

- Koleff, P., Gaston, K. J., & Lennon, J. J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72(3), 367-382. doi:10.1046/j.1365-2656.2003.00710.x
- Kondrak, G., & Sherif, T. (2006). Evaluation of Several Phonetic Similarity Algorithms on the Task of Cognate Identification. *Computational Linguistics*, 43–50.
- Lakatos, I. (1977). Science and pseudoscience. In *Philosophical Papers* (Vol. 1, pp. 1– 7). Cambridge: Cambridge University Press.
- Lee, S., & Hasegawa, T. (2011). Bayesian phylogenetic analysis supports an agricultural origin of Japonic languages. *Proceedings of the Royal Society of London B Biological Sciences*, 278(1725), 3662–3669. doi:10.1098/rspb.2011.0518
- Lee, S., & Hasegawa, T. (2013). Evolution of the Ainu language in space and time. *PLOS ONE*, 8(4), e62243. doi:10.1371/journal.pone.0062243.s005
- Lemey, P., Rambaut, A., Welch, J. J., & Suchard, M. A. (2010). Phylogeography takes a relaxed random walk in continuous space and time. *Molecular Biology and Evolution*, 27(8), 1877–1885. doi:10.1093/molbev/msq067
- Lemmon, A., & Lemmon, E. M. (2008). A likelihood framework for estimating phylogeographic history on a continuous landscape. *Systematic Biology*, 57(4), 544–561. doi:10.1080/10635150802304761
- Levinson, S. C., & Gray, R. D. (2012). Tools from evolutionary biology shed new light on the diversification of languages. *Trends in Cognitive Sciences*, 16(3), 167– 173. doi:10.1016/j.tics.2012.01.007
- Li, W. L. S., & Drummond, A. J. (2012). Model averaging and Bayes factor calculation of relaxed molecular clocks in Bayesian phylogenetics. *Molecular Biology and Evolution*, 29(2), 751–761. doi:10.1093/molbev/msr232

- Losos, J. B., & Ricklefs, R. E. (2009). Adaptation and diversification on islands. Nature, 457(7231), 830–836. doi:10.1038/nature07893
- Mace, R., & Jordan, F. M. (2011). Macro-evolutionary studies of cultural diversity: a review of empirical studies of cultural transmission and cultural adaptation. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 366(1563), 402–411. doi:10.1098/rstb.2010.0238
- Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, 27(2 Part 1), 209–220.
- Masuda, R., Amano, T., & Ono, H. (2001). Ancient DNA analysis of brown bear (Ursus arctos) remains from the archeological site of Rebun Island, Hokkaido, Japan. Zoological Science, 18(5), 741–751. doi:10.2108/zsj.18.741
- Mayr, E. (1998). This is biology. Cambridge: Harvard University Press.
- McElreath, R., Boyd, R., & Richerson, P. J. (2003). Shared norms and the evolution of ethnic markers. *Current Anthropology*, 44(1), 122–130. doi:10.1086/345689
- Moon, J., Hirose, N., Yoon, J., & Pang, I. (2009). Effect of the along-strait wind on the volume transport through the Tsushima/Korea Strait in September. *Journal of Oceanography*, 65(1), 17–29. doi:10.1007/s10872-009-0002-3
- Mufwene, S. S. (2008). *Language evolution: contact, competition and change*. London: Continuum International Publishing Group.
- Muromachi Jidaigo Jiten Henshū Iinkai. (2001). *Jidaibetsu kokugo daijiten: Muromachi jidai hen*. Tokyo: Sanseidō.
- Nakahashi, T. (2005). Nibonjin no kigen. Tokyo: Kodansha.

- Nekola, J. C., & White, P. S. (1999). The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, *26*(4), 867–878. doi:10.1046/j.1365-2699.1999.00305.x
- Nettle, D. (1998). Explaining global patterns of language diversity. *Journal of Anthropological Archaeology*, 17(4), 354–374. doi:10.1006/jaar.1998.0328
- Nettle, D. (1999). Is the rate of linguistic change constant? *Lingua*, 108(2), 119–136. doi:10.1016/S0024-3841(98)00047-3
- Nettle, D., & Dunbar, R. I. M. (1997). Social markers and the evolution of reciprocal exchange. *Current Anthropology*, *38*(1), 93–99.
- Nettle, D., & Harriss, L. (2003). Genetic and linguistic affinities between human populations in Eurasia and West Africa. *Human Biology*, 75(3), 331–344. doi:10.1353/hub.2003.0048
- Nettle, D., Grace, J. B., Choisy, M., Cornell, H. V., Guégan, J.-F., & Hochberg,
  M. E. (2007). Cultural Diversity, Economic Development and Societal
  Instability. *PLOS ONE*, 2(9), e929. doi:10.1371/journal.pone.0000929.t001
- Newton, M. A., & Raftery, A. E. (1994). Approximate Bayesian inference with the weighted likelihood bootstrap. *Journal of the Royal Statistical Society: Series B* (*Statistical Methodology*), 56, 3–48.
- Ogata, Y. (1989). A Monte Carlo method for high dimensional integration. Numerische Mathematik, 55(2), 137–157.
- Ohyi, H. (1985). On the process of crystallization of Sakhalin Ainu. Bulletin of the Institute for the Study of North Eurasian Cultures, Hokkaido University, 17, 165–192.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., O'Hara, R. B., Simpson, G. L., et al. (2013). vegan: Community Ecology Package. R package version 2.0-7.

- Omlin, M., & Reichert, P. (1999). A comparison of techniques for the estimation of model prediction uncertainty. *Ecological Modelling*, 115(1), 45–59. doi:10.1016/S0304-3800(98)00174-4
- Oota, H., Settheetham-Ishida, W., Tiwawech, D., Ishida, T., & Stoneking, M. (2001). Human mtDNA and Y-chromosome variation is correlated with matrilocal versus patrilocal residence. *Nature Genetics*, 29(1), 20–21. doi:10.1038/ng711
- Pagel, M. (2000). Maximum-likelihood models for glottochronology and for reconstructing linguistic phylogenies. In C. Renfrew, A. McMahon, & L. Trask (Eds.), *Time depth in historical linguistics* (Vol. 2, pp. 189–207). Cambridge: McDonald Institute for Archaeological Research.
- Pagel, M. (2009). Human language as a culturally transmitted replicator. *Nature Reviews Genetics*, 10(6), 405–415. doi:10.1038/nrg2560
- Pagel, M., & Mace, R. (2004). The cultural wealth of nations. *Nature*, *428*(6980), 275–278. doi:10.1038/428275a
- Pagel, M., Atkinson, Q. D., & Meade, A. (2007). Frequency of word-use predicts rates of lexical evolution throughout Indo-European history. *Nature*, 449(7163), 717–720. doi:10.1038/nature06176
- Pagel, M., Atkinson, Q. D., Calude, A. S., & Meade, A. (2013a). Reply to Mahowald and Gibson and to Heggarty: No problems with short words, and no evidence provided. *Proceedings of the National Academy of Sciences of the United States of America*, 110(35), E3255–E3255. doi:10.1073/pnas.1309838110
- Pagel, M., Atkinson, Q. D., Calude, A., & Meade, A. (2013b). Ultraconserved words point to deep language ancestry across Eurasia. *Proceedings of the National Academy of Sciences of the United States of America*. doi:10.1073/pnas.1218726110

- Paradis, E., Baillie, S. R., & Sutherland, W. J. (2002). Modeling large-scale dispersal distances. *Ecological Modelling*, 151(2-3), 279–292. doi:10.1016/S0304-3800(01)00487-2
- Paradis, E., Claude, J., & Strimmer, K. (2004). APE: Analyses of Phylogenetics and Evolution in R language. *Bioinformatics*, 20(2), 289–290. doi:10.1093/bioinformatics/btg412
- Parent, C. E., Caccone, A., & Petren, K. (2008). Colonization and diversification of Galapagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 363(1508), 3347–3361. doi:10.1016/S0169-5347(00)01930-3
- Peakall, R., & Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel.
  Population genetic software for teaching and research--an update. *Bioinformatics*, 28(19), 2537–2539. doi:10.1093/bioinformatics/bts460
- Penny, D., McComish, B., Charleston, M., & Hendy, M. (2001). Mathematical elegance with biochemical realism: the covarion model of molecular evolution. *Journal of Molecular Evolution*, 53(6), 711–723. doi:10.1007/s002390010258

Popper, K. (1992). The logic of scientific discovery. New York: Routledge.

- Posada, D. (2003). Selecting models of evolution. In *The phylogenetic handbook*. *A practical approach to DNA and protein phylogeny*. (256-282). Cambridge: Cambridge University Press.
- Posada, D., & Buckley, T. (2004). Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, 53(5), 793–808. doi:10.1080/10635150490522304

- Pybus, O. G., Suchard, M. A., Lemey, P., Bernardin, F. J., Rambaut, A., Crawford,
  F. W., et al. (2012). Unifying the spatial epidemiology and molecular evolution of emerging epidemics. *Proceedings of the National Academy of Sciences*, 1–12. doi:10.1073/pnas.1206598109
- Quintana-Murci, L., Krausz, C., Zerjal, T., Sayar, S. H., Hammer, M. F., Mehdi, S.
  Q., et al. (2001). Y-chromosome lineages trace diffusion of people and
  languages in southwestern Asia. *The American Journal of Human Genetics*, 68(2),
  537–542. doi:10.1086/318200
- R Core Team. (2013). R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. Retrieved from http://www.R-project.org
- Reali, F., & Griffiths, T. L. (2009). Words as alleles: connecting language evolution with Bayesian learners to models of genetic drift. *Proceedings of the Royal Society of London B Biological Sciences*, 277(1680), 429–436. doi:10.1098/rspb.2009.1513
- Renfrew, C. (1989). Models of change in language and archaeology. *Transactions of the Philological Society*, 87(2), 103–155. doi:10.1111/j.1467-968X.1989.tb00622.x
- Reynolds, A. M., & Rhodes, C. J. (2009). The Lévy flight paradigm: random search patterns and mechanisms. *Ecology*, *90*(4), 877–887. doi:10.1890/08-0153.1
- Ringe, J., & Donald, A. (1995). "Nostratic" and the factor of chance. *Diachronica*, *12*(20), 55–74. doi:10.1075/dia.12.1.04rin
- Roberts, S., & Winters, J. (2013). Linguistic diversity and traffic accidents: lessons from statistical studies of cultural traits. *PLOS ONE*, 8(8), e70902. doi:10.1371/journal.pone.0070902.s001

- Rogers, D. S., & Ehrlich, P. R. (2008). Natural selection and cultural rates of change. *Proceedings of the National Academy of Sciences of the United States of America*, 105(9), 3416–3420. doi:10.1073/pnas.0711802105
- Ross, R. M., Greenhill, S. J., & Atkinson, Q. D. (2013). Population structure and cultural geography of a folktale in Europe. *Proceedings of the Royal Society of London B Biological Sciences*, 280(1756), 20123065–20123065. doi:10.1098/rspb.2012.3065
- Rzeszutek, T., Savage, P. E., & Brown, S. (2012). The structure of cross-cultural musical diversity. *Proceedings of the Royal Society of London B Biological Sciences*, 279(1733), 1606–1612. doi:10.1098/rspb.2011.1750
- Saitou, N., & Nei, M. (1987). The neighbor-joining method: a new method for reconstructing phylogenetic trees. *Molecular Biology and Evolution*, 4(4), 406– 425.
- Sato, T., Amano, T., Ono, H., Ishida, H., Kodera, H., Matsumura, H., et al.
  (2007). Origins and genetic features of the Okhotsk people, revealed by ancient mitochondrial DNA analysis. *Journal of Human Genetics*, 52(7), 618–627. doi:10.1007/s10038-007-0164-z
- Sato, T., Amano, T., Ono, H., Ishida, H., Kodera, H., Matsumura, H., et al.
  (2009). Mitochondrial DNA haplogrouping of the Okhotsk people based on analysis of ancient DNA: an intermediate of gene flow from the continental Sakhalin people to the Ainu. *Anthropological Science*, (0), 905260063. doi:10.1537/ase081202
- Schleicher, A. (1869). *Darwinism tested by the science of language*. London: John Camden Hotten.
- Schwartz, G. H. (1978). Estimating the dimension of a model. Annuals of Statistics, 6, 461–464.

- Sereno, M. I. (1991). Four analogies between biological and cultural/linguistic evolution. *Journal of Theoretical Biology*, 151(4), 467–507. doi:10.1016/S0022-5193(05)80366-2
- Shibatani, M. (1990). *The languages of Japan*. New York: Cambridge University Press.
- Shimoji, M., & Pellard, T. (Eds.). (2010). *An Introduction to Ryukyuan Languages* (pp. 1–258). Retrieved from http://lingdy.aacore.jp/jp/material/An\_introduction\_to\_Ryukyuan\_languages.p df
- Sinsheimer, J. S., Lake, J. A., & Little, R. J. A. (1996). Bayesian hypothesis testing of four-taxon topologies using molecular sequence data. *Biometrics*, 52, 193–210.
- Smits, G. (1999). Visions of Ryukyu: identity and ideology in early-modern thought and politics. University of Hawaii Press.
- Smouse, P. E., Long, J. C., & Sokal, R. R. (1986). Multiple regression and correlation extensions of the Mantel test of matrix correspondence. *Systematic Zoology*, 35(4), 627–632.
- Sober, E. (1975). Simplicity. Oxford University Press.
- Sober, E. (1991). Reconstructing the past. MIT Press.
- Sokal, R. R., & Thomson, B. A. (1998). Spatial genetic structure of human populations in Japan. *Human Biology*, 70(1), 1–22.
- Starostin, S. A., Dybo, A. V., & Mudrak, O. A. (2003). *Etymological dictionary of the Altaic languages*. Brill Academic Publishers.
- Steel, M. (2005). Should phylogenetic models be trying to "fit an elephant"? *Trends in Genetics*, 21, 307–309. doi:10.1016/j.tig.2005.04.001

- Sterman, J. D. (2002). All models are wrong: reflections on becoming a systems scientist. *System Dynamics Review*, 18(4), 501–531. doi:10.1002/sdr.261
- Suchard, M. A., Weiss, R. E., & Sinsheimer, J. S. (2001). Bayesian selection of continuous-time Markov chain evolutionary models. *Molecular Biology and Evolution*, 18(6), 1001–1013. doi:10.1093/oxfordjournals.molbev.a003872
- Suzuki, H. (1981). Racial history of the Japanese. *Rassengeschichte Der Menschheit*, 8, 7–69.
- Swadesh, M. (2006). *The origin and diversification of language*. (J. F. Sherzer, Ed.). New Brunswick: Transaction Publishers.
- Tajima, A., Hayami, M., Tokunaga, K., Juji, T., Matsuo, M., Marzuki, S., et al.
  (2004). Genetic origins of the Ainu inferred from combined DNA analyses of maternal and paternal lineages. *Journal of Human Genetics*, 49(4), 187–193.
  doi:10.1007/s10038-004-0131-x
- Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift Fur Tierpsychologie, 20(4), 410-433. doi:10.1111/j.1439-0310.1963.tb01161.x
- Turner, C. G. II. (1986). Dentochronological separation estimates for Pacific Rim populations. *Science*, 232(4754), 1140. doi:10.1126/science.232.4754.1140
- Turner, C. G. II. (1990). Major features of Sundadonty and Sinodonty, including suggestions about East Asian microevolution, population history, and late Pleistocene relationships with Australian aboriginals. *American Journal of Physical Anthropology*, 82(3), 295–317. doi:10.1002/ajpa.1330820308
- Vovin, A. (1993). A reconstruction of proto-Ainu. Leiden: Brill.
- Wade, P. R. (2000). Bayesian methods in conservation biology. *Conservation Biology*, 14(5), 1308–1316. doi:10.1046/j.1523-1739.2000.99415.x

- Walker, R. S., & Ribeiro, L. A. (2011). Bayesian phylogeography of the Arawak expansion in lowland South America. Proceedings of the Royal Society of London B Biological Sciences, 278(1718), 2562–2567. doi:10.1098/rspb.2010.2579
- Wen, B., Li, H., Lu, D., Song, X., Zhang, F., He, Y., et al. (2004). Genetic evidence supports demic diffusion of Han culture. *Nature*, 431(7006), 302–305. doi:10.1038/nature02878
- Whitman, J. (1985). The phonological basis for the comparison of Japanese and Korean.(Unpublished doctoral dissertation). Harvard University.
- Wintle, B. A., McCarthy, M. A., Volinsky, C. T., & Kavanagh, R. P. (2003). The use of Bayesian model averaging to better represent uncertainty in ecological models. *Conservation Biology*, 17(6), 1579–1590.
- Yamaguchi-Kabata, Y., Nakazono, K., Takahashi, A., Saito, S., Hosono, N., Kubo, M., et al. (2008). Japanese population structure, based on SNP genotypes from 7003 individuals compared to other ethnic groups: effects on population-based association studies. *The American Journal of Human Genetics*, *83*(4), 445–456. doi:10.1016/j.ajhg.2008.08.019
- Yang, Z. (1996). Among-site rate variation and its impact on phylogenetic analyses. *Trends in Ecology and Evolution*, 11, 367–372. doi:10.1016/0169-5347(96)10041-0