A phylogenetic analysis of dispersal norms, descent and subsistence in Sino-Tibetans

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Abstract

Sex-specific dispersal have long been of interest to anthropologists and biologists, as they structure populations and determine patterns of kinship, relatedness and cooperation. In most contemporary human societies, females usually disperse at marriage. In a minority of human societies, male disperse, bisexual philopatry or disperse are practiced. Previous studies suggest that emergence of agriculture, cattle pastoralism, or patriliny is associated with female-biased dispersal in certain language families. The ancestral patterns of sex-specific dispersal and its ecological correlates in Sino-Tibetans remain uncertain. Here we use comparative phylogenetic methods to infer the evolutionary history of sex-specific dispersal in Sino-Tibetan speakers, and tested for coevolution between subsistence (intensive agriculture and cattle pastoralism), descent and sexspecific dispersal patterns. We use a variety of ethnographic and historical sources to identify dispersal strategies across Sino-Tibetan phylogenetic trees (n=97). We found that 1) earliest Sino-Tibetan speakers were likely patrilocal; 2) intensive agriculture is associated with both female and male dispersal patterns, although there is no evidence showing transition from non-intensive agriculture to intensive agriculture promotes "female disperse"; 3) cattle pastoralism is not correlated with dispersal patterns of both sexes; and 4) descent is associated with female dispersal, but not male dispersal. Moreover, change from state of "non-patrilineal" to "patrilineal" triggered change in female's dispersal patterns, from "female non-disperse" to "female disperse". Our results suggest that change in descent, not intensive agriculture, drove change in female-specific dispersal in Sino-Tibetans. Our findings illustrated how subsistence or descent can play different roles in shaping sex-biased dispersal patterns.

Key words: sex-biased dispersal, Sino-Tibetan, cultural phylogenetics, ancestral states, coevolution, intensive agriculture, descent

1. Introduction

Sex-biased dispersal, i.e. sex differences in migration from birth place to breeding location, is common in mammals, birds, insects, and humans (Greenwood, 1980; Li & Kokko, 2019; Pusey, 1987; Wood et al., 1985). A global genetic study of sex-specific transmission in humans using mitochondrial DNA (mtDNA) and Y chromosome suggested a higher dispersal rate in females than in males, i.e. a prevalence of patrilocality (Oota et al., 2001; Seielstad et al., 1998). However, in some cultures, residence is much more flexible. For example, contemporary forager societies often show flexible residence with bisexual philopatry or dispersal, couples often change their residence from time to time (Hill et al., 2011; Marlowe, 2004). Whereas horticulturalists were either found to be more patrilocal (Wood et al., 1985), or more uxorilocal than hunter-gatherers (Walker et al., 2013). What predicts residence patterns, and the evolutionary history of sex-specific dispersal have long been of interest to anthropologists, as they structure populations and determine patterns of kinship, relatedness and cooperation.

Various approaches have been applied to investigate the ancestral state of sex-specific dispersal in early human history. Through isotopic analyses, archaeological studies proposed that femalebiased dispersal in early and late Neolithic Europe (Haak et al., 2008; Bentley et al., 2012; Bentley, 2013; Sjögren et al., 2016), while in Thailand, the stable isotopes evidence supported for malebiased dispersal in 2000 BC (Bentley et al., 2005). By mapping ethnographic data on kinship systems onto linguistic phylogenetic trees, phylogenetic comparative methods became a powerful tool to make inferences about the pattern of cultural evolution, including ancestral states, patterns of historical change, and coevolution of kinship and ecological and social variables (Holden & Mace, 2003; Mace & Pagel, 1994; Pagel, 1994). Cultural phylogenetic comparative methods have previously been applied to questions on the evolution of kinship systems, particularly post-marital residence and descent (see SI Glossary) in several linguistic populations. These studies suggested Proto-Indo-European was virilocal or neolocal (Fortunato, 2011; Fortunato & Jordan, 2010), proto-Malayo-Polynesian was uxorilocal, and matrilocality was prevailing in proto-Austronesian populations (Fortunato & Jordan, 2010; Jordan et al., 2009). A phylogenetic study using linguistic data from five large language families (Austronesian, Bantu, Indo-European, Pama-Nyungan, and Uto-Aztecan) suggested that evolutionary trajectories of post-marital residence systems are likely to vary with each language family (Moravec et al., 2018).

Some light has also been shed on the coevolution of sex-specific dispersal and various ecological or social factors. Holden and Mace tested for coevolution between cattle and descent in Bantu-speaking cultures, and found acquiring cattle led to the loss of matrilineal descent (Holden & Mace, 2003). Food producing populations (agriculturalists and pastoralists) have a higher ratio of mtDNA/Y chromosome diversity than hunter-gatherers, suggesting that patrilocality and more female migration in the former (Destro-Bisol et al., 2004). The association between sex-specific migration and mode of subsistence has led to the hypothesis that the transition from foraging to agriculture and/or animal husbandry played an important role in promoting female-biased dispersal (Marlowe, 2004; Wilkins, 2006; Wilkins & Marlowe, 2006). Resteiro and colleagues tested the hypothesis using theoretical simulation, and found that patrilocality in farmers explains the present patterns of genetic diversity better than other residence rules (Rasteiro et al., 2012). A recent cultural phylogenies of a global super-tree including 290 language populations has shown that intensive agriculture, large domestic animals, and plough agriculture all hindered matrilocality (Surowiec et

al., 2019). On the other hand, an archaeological study in Thailand implies a male-biased dispersal (matrilocal) system during the period of the introduction and intensification of agriculture, providing a likely antithesis (Bentley et al., 2005). Social structures, such as descent, also shape sex-specific dispersal. Strong correlations between residence and descent were found in different studies (Surowiec et al., 2019; Opie et al., 2014; Jordan, 2007), although the co-evolutionary trend between two cultural traits varies in each language family.

The Sino-Tibetan language family is one of the largest language families in the world in the number of speakers (LaPolla, 2006; Matisoff, 1991). Despite widespread norms of female-biased dispersal in Sino-Tibetan regions, multilocal, uxorilocal, and duolocal residence have a long history and have being practiced by around 14% of all societies (Figure 1). The evolutionary history of sexspecific dispersal of Sino-Tibetans attracted much attention. Some evidence on ancestral patterns of dispersal and residence is now becoming available from linguistic, genetic and archaeological studies, although findings are contradictory.

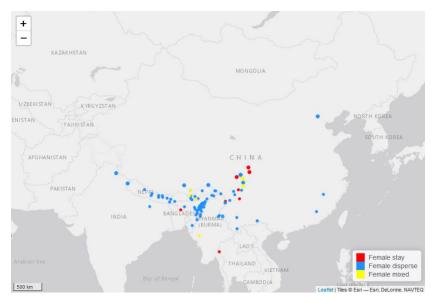


Figure 1. Geographical distribution of norms of female-specific dispersal systems across Sino-Tibetan societies sampled in this study (WorldGeoDatasets, 2017). Blue is where female disperse at marriage, pink is where female stay at marriage, and yellow is females either disperse or stay.

Linguistic studies on kinship terminologies of Himalayan languages (Vinding, 1979) and Burmish languages (Bradley, 1989) regarding post-marital residence and preferred direction of cousin marriage suggested a predominantly patrilocal proto-Sino-Tibetan society base. While archaeological and genetic studies provide mixed conclusions. Sites of Yangshao culture (5000~3000 B.C.) and Hongshan culture (4500~2500 B.C.), such as Jiangzhai and Niuheliang, are often interpreted as egalitarian, matrilineal societies based on the layout of burial sites, feminine figurines and female-biased distribution of burial goods (Feng, 2013; Nelson & Rosen-Ayalon, 2001). However, a study concentrated on the biological characteristics and sex ratio of the graves of Shijia (Yangshao culture around 4000 B.C.) concluded that residency was most likely patrilocal (Gao & Lee, 1993). The Fujia community of Dawenkou culture in China (circa. 2800-2500 B.C.) is thought likely to have been matrilocal due to the low mtDNA diversity and relatively high diversity of Y-chromosomes in a burial site excavation (Dong et al., 2015). However, this contrasts with the patrilocal burial patterns found in the later Shang dynasty (circa. 1600-1046 B.C.) (Chang et al., 2005). A genetic study of the matrilineal Mosuo suggested that matriliny arose in the late Neolithic (Lu et al., 2012), but the confidence intervals on estimated dates are wide, so it is hard to link to the emergence of matriliny to particular clades. Other genetic evidence showed that Y haplotypes of Han Chinese vary little across China but mtDNA has a clear North-South divide, suggesting that male-led southward migrations of Han during warfare over the last 1200 years could have introduced male-centered kinship systems (i.e. patrilocality) to historically matrilocal groups in southwestern China (Wen et al., 2004).

Despite these advances, there is no agreement with the evolutionary history of sex-specific dispersal of Sino-Tibetans, nor formal test assessing the factors influencing sex-specific dispersal. Also, females' and males' dispersal patterns are usually considered as interchangeable with residence in earlier studies, although it is not always the case. For example, male immigration is strictly controlled in some patrilocal populations (Hamilton et al., 2005), but is as flexible as in matrilocal populations in other patrilocal populations (Ly et al., 2018). The demographic history and genetic flow can be different in males and females (Bentley et al., 2009; Cavalli-Sforza, 1998), implying sex-specific models are needed to fully understand the evolution of human dispersal. Here we analyze the evolutionary history of marital dispersal norms in females and males in the Sino-Tibetans, using cultural phylogenetic comparative methods. And we test the coevolution of sex-specific dispersal and subsistence (i.e. intensive agriculture and/or cattle pastoralism) and descent.

2. Data and Methods

2.1. Phylogeny

We used the most comprehensive Sino-Tibetan phylogeny available to date based on linguistic data from 131 Sino-Tibetan languages (Zhang et al., 2020). After burn-in, a sample of 901 trees was taken from the Bayesian posterior distribution of Sino-Tibetan phylogeny. Trees were pruned to 97 languages and 95 languages for which ethnographic data on sex-specific dispersal, subsistence and descent were available.

2.2. Ethnographic data and coding

2.2.1. Ethnographic data

Ethnographic data on post-marital residence, descent and subsistence of Sino-Tibetan groups were obtained from ethnographic publications, government censuses, World culture Encyclopaedia (<u>www.everyculture.com</u>), Murdock's *Ethnography Atlas* (Murdock, 1967), and historical records where possible. References to proto-Sino-Tibetan groups in historical records dated from 109 B.C. to 1370 A.D. were accessed via 中華經典古籍庫 (Zhonghua Ancient Books Database) at <u>http://publish.ancientbooks.cn/docShuju/platformSublibIndex.jspx?libId=6</u>. If more than one type of residence rules or descent are implemented in a group, the primary type was used for analysis. 14 groups in the *Ethnography Atlas* were independently corroborated with data extracted from various sources, 3 groups are collected just from EA, other 81 groups are from various resources. The ethnographic and historical sources are shown in the SI.

2.2.2. Coding of ethnographic data

Sex-specific dispersal was decoded from norms of post-marital residence. Specifically, in

patrilocal and neolocal, females disperse at marriage (female disperse), in matrilocal and duolocal, females do not disperse (females stay). In ambilocal or bilocal, females either stay or disperse (females mixed). One the other hand, males stay in patrilocal and duolocal (male stay), and they disperse in matrilocal and neolocal (male disperse). While in ambilocal or bilocal, males either stay or disperse (males mixed). We distinguished patrilineal, matrilineal and mixed (ambilineal or others) descent. Some ethnographies mentioned local beliefs (or the ethnographer's own belief) of matrilocal antiquity; but we only categorize nodes as female-stay norm when precise chronological and geographical information appear repeatedly in historical records. All data are coded independently by two researchers. To make sure the results is not affected by coding strategy, the binary dispersal data is coded as disperse/non-disperse (including female stay and female mixed) and stay/non-stay (including female disperse and female mixed), the descent is coded as patrilineal/non-patrilineal and matrilineal/non-matrilineal in co-evolution analysis, respectively. Coding for subsistence follows EA C7 (subsistence economy contributes most) and C39 (Predominant type of animal husbandry). In coevolution analysis, the data on agriculture is coded as intensive agriculture/non-intensive agriculture, and the data on predominant type of animal husbandry is coded as cattle/non-cattle.

2.3. Comparative analyses of sex-specific dispersal

2.3.1. Ancestral states of sex-specific dispersal

We inferred the ancestral states of dispersal and rates of transitions between different states using Bayesian RJMCMC methods (Pagel, 1994; Pagel et al., 2004; Pagel & Meade, 2006) as implemented in *BayesTraits* (www.evolution.reading.ac.uk). These methods derived the parameters of models of trait evolution, while simultaneously accounting for uncertainty in the phylogeny, by integrating models over the posterior sample of 901 trees. We employed the "most-recent-common-ancestor" approach (Pagel et al., 2004), to find the node in each tree in the posterior sample that contains a given set of descendant taxa, and calculates the ancestral value at that node.

Internal nodes can be fixed as either state where historical records give independent information about the ancestral state, by applying the "Fossil" command in BayesTraits v3. This function is also a useful way to test if one state receives better support than the other at various ancestral nodes. Support for different RJMCMC models were compared using log Bayes Factor (log BF), a Log Bayes Factor between 2-5 indicates positive evidence, 5-10 indicates strong evidence, and larger than 10 indicates very strong evidence (Pagel et al., 2004; Pagel & Meade, 2006).

The model of trait evolution is a continuous-time Markov model as described by Pagel (1994) with rate parameters recording transitions to and from the two states of each trait (Pagel, 1994). We used empirical base frequencies to scale the transition rates, and we used a uniform hyperprior with a mean and variance in the range of 0-10 to seed an exponential distributed transition rates prior. The RJMCMC was run for 20,050,000 iterations and was sampled every 1,000th iteration, with a burn-in period of 50,000 iterations, produced a posterior sample of 20,000. We run each RJMCMC five times.

2.3.2. Coevolution between sex-specific dispersal, subsistence and descent

We have tested the correlated evolution between sex-specific dispersal, descent and two types of subsistence, intensive agriculture and cattle pastoralism pairwise. The analyses are performed in Discrete implemented in BayesTraits v3. We run the independent model in which the two traits evolve independently, and the dependent model in which the two traits are correlated. The priors were drawn from exponential hyperpriors with a mean and variance between 0-10. Each RJMCMC was run for 10,000,000 iterations and was sampled every 1,000, with the first 50,000 iterations discarded as the burn-in period. We use Log Bayes Factor to explore whether dependent models are significantly better than independent model. We have repeated coevolution analysis with various coding. The result is considered as significant only if it received positive support from analysis with both coding strategies.

The maximum clade credibility tree was derived using TreeAnnotator v1.8.4 (Drummond & Rambaut, 2007). Figures are produced with *leaflet* (Cheng et al., 2019), *ape* (Paradis et al., 2004) and *ggplot2* (Wickham, 2016) packages in RStudio (<u>http://www</u>.rstudio.com/) software. Other statistical analyses are carried out in Tracer V1.6 (Rambaut et al., 2018) and Rstudio.

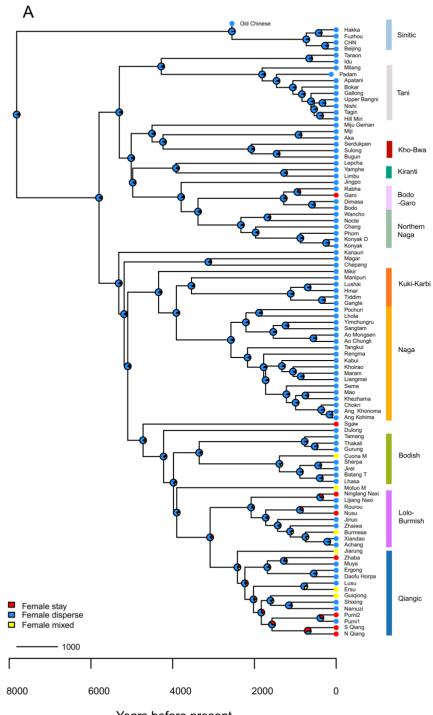
3. Results

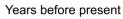
3.1. The ancestral states of sex-specific dispersal in Sino-Tibetans

Among all the Sino-Tibetan language groups that we can identify their norms of marital residence, over 85% of them practice female disperse at marriage (n=83). In these societies, female either lives with husband's kin or moves to a new household established by the married couple. Females do not disperse at marriage (as in matrilocal or duolocal residence) in about 8% of all societies (n=8), whereas about 6% of the societies lack of strict norms on whether women should disperse or not (n=6). Dispersal norms for males in Sino-Tibetan are distinct from that for females. Males disperse in 24.7% of all societies (n=24), whereas in 59.8% groups males stay in natal household after marriage (n=58), where the post-marital residence is either patrilocal or duolocal. About 15% of the societies has no rules about whether men should disperse or not (n=15). Hence, dispersal norm is less restricted for males than for females in Sino-Tibetans.

We reconstructed ancestral states of both female and male dispersal norms at the root and each internal node of the Sino-Tibetan linguistic phylogeny, using a Bayesian RJMCMC method (Pagel & Meade, 2006). The transition rates between different states in females and males on the branches of a set of phylogenies are also estimated respectively.

The predicted ancestral states for dispersal norms for female and male in Sino-Tibetans are shown in Figure 2. Results show the ancestral state at the root of Sino-Tibetan is females disperse (Prob=0.8541, sd=0.0005, 95% HPD Interval [0.8488, 0.9124]) and males stay (p=0.5991, sd=0.0001, HPD Interval [0.5974, 0.6036]). Our results indicate a possible patrilocal residence in Proto-Sino-Tibetans. Female dispersal norm has a long history in Sino-Tibetans, and the derived traits of females staying or a mixed strategy evolved in only a few groups later in history. In contrast, male dispersal pattern is more variable, although males staying is ancestral, the derived trait of male disperse also appeared in many groups in Sino-Tibetans.





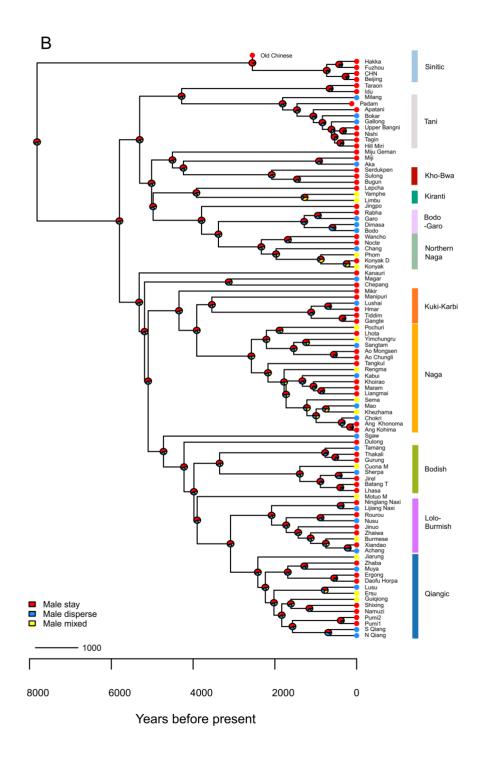


Figure 2. Ancestral states for female dispersal (A) and male dispersal (B) at marriage in the Sino-Tibetan language family. The maximum clade credibility trees summarize the final posterior sample of 901 phylogenetic trees. Circles at nodes indicate proportional levels of support for the three alternative dispersal systems under the best-fitting model. Branch lengths are proportional to

time. Red indicates stay at marriage, blue indicates disperse, and yellow indicates either stay or disperse. Old Chinese and Padam are extinct languages.

We estimated the posterior distributions of transition rates from one dispersal state to another in both sexes (Figure 3). We found that the changes between disperse to stay in females and males happened in both directions in Sino-Tibetan history. Furthermore, the changes between females disperse and female mixed are slightly less likely to happen, and we found no support for the transition between females stay and females mixed (Figure 3A). While in males, the only significant change is between males disperse and males stay. Change between males disperse and mixed, or between males stay and mixed are unlikely to happen (Figure 3B).

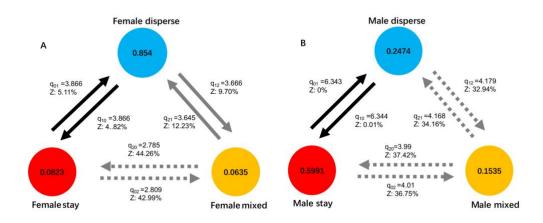


Figure 3. Transition rates between different states in females' (A) and males' (B) dispersal patterns. Z indicates how many times the transition rates are estimated to be 0.

In an additional analysis, by fixing the value of a focal node either as female disperse, female stay or mixed, and comparing the log marginal likelihood pairwise (log BF), we tested which state is more likely to be ancestral at the root, the outgroup (Node 93 Sinitic) and at three internal nodes where female stay or mixed norms assembled (Node 23 Lolo-Burmish and Qiangic, Node 32 Bodish, Node 73 Bodo-Garo) (Table 1). We found positive support for female disperse at marriage being the ancestral state at the root of the whole tree (Root), and at all the internal nodes that tested. These results confirm that female disperse was established early in the Sino-Tibetans and in these internal groups. This result is in accordance with ethnographic accounts that a small matrilineal Himalayan group Garo adopted the matrilineal social system a few generations before the beginning of the colonial period in the 19th century (von ehrenfels, 1971). Our findings support female dispersal at the MRCAs of Lolo-Burmish and Qiangic groups (Node 23), and of Bodic (Node 32). Therefore, the female staying norms in some Lolo-Burmish and Qiangic groups and female mixed norms in some Bodish groups all have a short history.

Table 1. Log marginal likelihood of each node with fixed female dispersal state and log BF between two models with different states.

Fixed	Description of the node Log marginal likelihood when				Log BF		
nodes	fixed as female						
		Stay	Disperse	Mixed	(2,1)	(1,3)	(2,3)

		(1)	(2)	(3)			
Node 1	Root	-53.96	-51.67	-54.28	4.58	0.65	5.23
Node 23	MRCA of Lolo-Burmish	-53.33	-51.92	-53.60	2.82	0.53	3.35
	and Qiangic						
Node 32	MRCA of Bodish	-53.90	-51.70	-53.66	4.39	-0.46	3.93
Node 73	MRCA of Bodo-Garo	-53.59	-51.70	-54.73	3.78	2.28	6.06
Node 93	MRCA of Sinitic	-58.30	-51.53	-58.63	13.54	0.67	14.21

3.2. Coevolution of sex-specific dispersal, subsistence and descent

As reported, prior studies have proposed that female-biased dispersal is associated with descent and mode of subsistence, such as spread of agriculture or cattle (Bentley et al., 2009; Hill et al., 2011; Holden & Mace, 2003; Marlowe, 2004; Opie et al., 2014; Wilkins & Marlowe, 2006). Here we tested the coevolution between subsistence (intensive agriculture, cattle), descent, and marital dispersal in both Sino-Tibetan males and females, by comparing the independent model and dependent model between two traits pairwise (Table 2). We also estimated the transition rates from one state to another, to determine the most possible evolutionary pathway.

In general, our results indicate that intensive agriculture significantly associated with both female and male dispersal in Sino-Tibetans. The correlation between intensive agriculture and female dispersal received very strong support, while coevolution of intensive agriculture and male dispersal is less strong, but still positive. However, no correlation between cattle and dispersal in both sexes were found, which suggests unlike in Bantu, adopting cattle did not affect the change of marital dispersal in Sino-Tibetans. More interestingly, descent is only significantly correlated with female dispersal, but not males (Table 2). Specifically, log BFs over 20 suggest decisive support for correlated evolution between descent and female dispersal norms. These results are not sensitive to the alternative coding strategies.

		Model	Female dispersal norms		Male dispersal norms	
			Disperse/	Stay/	Disperse	Stay/
			non-	non-	non-	non-
			disperse	stay	disperse	stay
Subsistence	Intensive	Independent	-86.77	-77.67	-106.21	-115.38
	agriculture	Dependent	-78.63	-73.18	-104.48	-113.53
		Log BF	16.27	8.97	3.45	3.70
	Cattle	Independent	-112.49	-100.97	-127.52	-134.17
		Dependent	-111.63	-103.46	-127.89	-137.47
		Log BF	1.72	-4.98	-0.74	-6.59
Descent	Patrilineal	Independent	-76.28	-68.59	-97.98	-104.93
	/non-	Dependent	-60.30	-54.69	-98.65	-107.07
	patrilineal	LogBF	31.97	27.79	-1.34	-4.29
	Matrilinea	Independent	-66.48	-56.98	-89.35	-94.00
	l/ non-	Dependent	-54.96	-44.75	-88.01	-96.19
	matrilineal	LogBF	23.05	24.45	2.67	-4.38

Table 2. Coevolution of female and	male dispersal and	l subsistence and	descent. Significant
effects are in bold.			

Transition rates indicate how changes happen between different states. Figure 4 shows the RJ analysis of coevolution between intensive agriculture and female and male dispersal patterns, as well as coevolution between descent and female dispersal pattern.

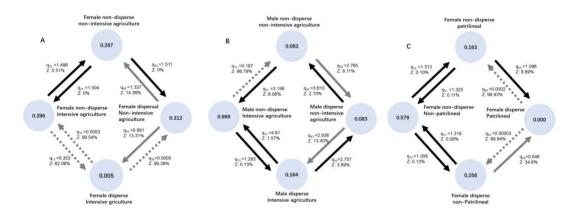


Figure 4. Estimated transition rates of coevolution between intensive agriculture and dispersal in females (A) and males (B), and between descent and female dispersal (C) across Sino-Tibetan phylogeny.

As shown in Figure 4A, the most stable state is "female disperse" and intensive agriculture, as the transition rates from this state to others are all very low. This implies that it is unlikely that females change their dispersal patterns from "disperse" to "stay" or "mixed" in agricultural societies. Although intensive agriculture is strongly correlated with female dispersal patterns, there is no evidence indicating that change of subsistence form "non-intensive agriculture" to "intensive agriculture" has driven change from "female non-disperse" to "female disperse" in Sino-Tibetans (Figure 4A), "female disperse" may have already existed before intensive agriculture has spread in Sino-Tibetans. Instead, the results suggest that "female non-disperse" in some agricultural Tibeto-Burman groups (Burmese, Ersu, Garo, Jiarung, Motuo_M, Ninglang_Naxi, Sgaw, and Zhaba), had to be evolved with "non-intensive agricultural" subsistence. These groups may have adopted intensive agriculture later. Similar pattern was found in the coevolution of intensive agriculture and descent in an additional analysis, which shows descent was associated with intensive agriculture, but not cattle (Table S1), and non-patrilineal descent can be only evolved in "non-intensive agriculture" societies (Figure S1).

Different pattern was found in coevolution of male dispersal and intensive agriculture. As shown in Figure 4B, the ancestral state is most likely to be "males stay" and intensive agriculture (P=0.6722). This state is slightly more stable than other three states. However, the switches between "male disperse" to "male non-disperse" occur frequently in agricultural societies, suggesting agricultural societies has less restrictions on males' residence than female's. From ancestral state of "male non-disperse" and "intensive agriculture" to derived state of "male disperse" and "non-intensive agriculture", the most possible pathway is males disperse first, and then subsistence change.

As described above, descent is only associated with female dispersal, rather than male. Notably, the transition rates indicate that change of descent from "non-patrilineal" to "patrilineal" may have

driven change of female dispersal from "non-disperse" to "disperse" in Sino-Tibetans (Figure 4C). Patrilineal and "female disperse" is the most stable state among all. From ancestral state of "female non-disperse" and non-patrilineal to derived state of "female disperse" and patrilineal, the route that descent change first is more likely. The result is partly consistent with what has been found in Bantu farmers (Opie et al., 2014; Surowiec et al., 2019).

4. Discussion

Our results suggest that "female disperse", and "male stay" were ancestral at the root of the Sino-Tibetan phylogeny. Changes between "disperse" and "stay" in both directions occurred during the evolution in both sexes, indicating unidirectional models of kinship evolution were not applicable to Sino-Tibetans. Our results concur with some Linguistic and archaeological findings suggesting that patrilocal in proto-Sino-Tibetan society (Bradley, 1989; Vinding, 1979), and matriliny may be relatively recent among Sino-Tibetans (Chang et al., 2005; Dong et al., 2017; Gao & Lee, 1993). For example, unlike the two other matrilineal Austro-Asiatic groups in India (i.e. Kerala and Khasi), the Sino-Tibetan Garo people believe that they adopted matrilineal system and female-biased dispersal only recently from the neighbouring Khasi; its male-dominant institutions and religious practices also hint closer historical relationship with patrilineal Assamese Highlanders (von ehrenfels, 1971).

Prior work has documented the association between subsistence and female-biased dispersal (Marlowe, 2004; Wilkins, 2006; Wilkins & Marlowe, 2006). Our results suggested strong correlations between intensive agriculture and both female and male dispersal patterns. However, we did not find support for the largely verbally expressed hypothesis that the adoption of intensive agriculture drove a change to female dispersal. Instead, we found change in female's dispersal pattern preceded the change from "non-intensive agriculture" to "intensive agriculture" in Sino-Tibetans. This result is consistent with a recent linguistic study which suggested Sino-Tibetan languages predates the major farming expansion in Sino-Tibetan regions by one to two millennia (Zhang et al., 2020). The state of "female disperse" and "intensive agriculture" appeared to be most stable, which implies female dispersal is strictly controlled in agricultural society, as they have little chance to change their dispersal patterns from disperse to non-disperse. In contrast, male dispersal is more flexible in agricultural societies, the results thus support the previous predictions using mitochondrial DNA and Y chromosome (Ly et al., 2018). Unlike finding from Bantu populations (Holden & Mace, 2003), no correlations between cattle and dispersal or descent were found in Sino-Tibetans.

Most notably, by analyzing cultural history of male and female dispersal separately, we found that descent is only associated with female dispersal, but not male. In addition, change from state of "non-patrilineal" to "patrilineal" triggered change in female dispersal patterns, from "female non-disperse" to "female disperse". These results challenge the "Main sequence theory" (Murdock, 1949), which suggests change of residence cause change of other social structure.

This is the first attempt to our knowledge to investigate sex-specific dispersal patterns in Sino-Tibetans using cultural phylogenetic methods. Our findings illustrated how subsistence and descent can play different role in shaping female and male dispersal patterns. These results extend prior work (Jordan, 2007; Opie et al., 2014; Surowiec et al., 2019). We found female non-dispersal is not ancestral, why did certain ethnolinguistic groups adopt such systems were not clear. However, our results imply that these derived traits such as female non-dispersal, male mixed dispersal patterns, or matrilineal descent should have been evolved in non-agricultural societies. Future studies will examine the coevolution of Sino-Tibetan dispersal systems with other possible ecological and social variables.

Data availability. The authors declare that data supporting the findings of this study are available within the paper and its Supplementary Information.

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