

# Evolutionary history of partible paternity in lowland South America

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**Partible paternity, the conception belief that more than one man can contribute to the formation of a fetus, is common in lowland South America and characterized by nonexclusive mating relationships and various institutionalized forms of recognition and investment by multiple cofathers. Previous work has emphasized the fitness benefits for women where partible paternity beliefs facilitate paternal investment from multiple men and may reduce the risk of infanticide. In this comparative study of 128 lowland South American societies, the prevalence of partible paternity beliefs may be as much as two times as common as biologically correct beliefs in singular paternity. Partible paternity beliefs are nearly ubiquitous in four large language families—Carib, Pano, Tupi, and Macro-Je. Phylogenetic reconstruction suggests that partible paternity evolved deep in Amazonian prehistory at the root of a tentative Je-Carib-Tupi clade. Partible paternity often occurs with uxorilocal postmarital residence (males transfer), although there are exceptions. Partible paternity may have benefits for both sexes, especially in societies where essentially all offspring are said to have multiple fathers. Despite a decrease in paternity certainty, at least some men probably benefit (or mitigate costs) by increasing their number of extramarital partners, using sexual access to their wives to formalize male alliances, and/or sharing paternity with close kin.**

Amazonia | human mating strategies | multiple fathers

**P**artible paternity refers to a conception belief common to indigenous populations in lowland South America (1, 2). According to this belief, more than one biological father contributes semen, which accumulates in the mother over time and helps create the fetus. This institutionalized recognition of multiple cofathers is sometimes accompanied by ritualized sequential sex (3–5), exchange of fish, meat, or gifts for sex (6–8), couvade practices performed by secondary fathers (3, 6, 9–13), and in both cases where it has been investigated, higher survival of offspring with a secondary father (1, 11).

Beckerman and Valentine (2) point to a continuum of paternity beliefs in lowland societies. In the simplest of schemes (Table 1), on the extreme singular paternity end, extramarital sex is considered immoral, behavior is prudish, and jealous men are more likely to commit violence against wives who engage in extramarital sex. In contrast, on the universal partible paternity end of the spectrum, nearly all offspring have purported multiple cofathers, extramarital relations are normal, and sexual joking is commonplace. One argument for this variation rests with an increasing degree of female sexual freedom or reproductive autonomy facilitated by uxorilocal residence where women often coreside with their parents and sisters. Uxorilocality may shift power relations in ways that favor greater female reproductive autonomy (2) and render mate guarding by males more difficult. Virilocal residence (females transfer), in contrast, may help facilitate stronger control by husbands over their wives' sexuality, although males might sometimes be more tolerant of extramarital relations if most paternity will be shared with close relatives. In addition, a female-biased sex ratio, perhaps linked with high mortality of males in warfare, may lead to more extramarital sex.

Mesoudi and Laland (14) modeled how female-biased sex ratios can drive the correlated evolution of partible paternity beliefs and more multiple mating behavior. However, in some cases, partible paternity is institutionalized in polyandrous marriages (e.g., Ache and Guaja) (15, 16) that likely result from male-biased sex ratios.

A societal belief in partible paternity may facilitate a woman's ability to simultaneously shop for good genes and solicit some paternal investment or social support from multiple men while minimizing the risk of infanticide and abuse (2, 17, 18). Partible paternity may be advantageous for women when the investment and support they receive from an individual husband quickly reaches diminishing returns. Various socioecological contexts have likely led to different manifestations of partible paternity in a constant negotiation between and among men and women over the assignment and acceptance of secondary fatherhood (2). It seems likely that men, especially those with higher status, could use partible paternity as an institution to increase their number of extramarital partners. Partible paternity may also serve as a form of hedging by males by dividing up potential paternity and investment across a wider number of offspring. Also, men may share their wives to formalize male alliances, analogous to wife exchange in other parts of the world (e.g., Inuit and Pagan Gaddang) (19, 20).

In this paper, we estimate the prevalence of partible paternity across lowland societies and outline the fitness benefits of partible paternity from both male and female perspectives. Using the suggestion by Hrdy (17, 18) and Beckerman and Valentine (2) that there is more female reproductive autonomy in female philopatric systems, we test the statistical relationship between uxorilocal residence and partible paternity beliefs. We also explicitly focus on phylogenetic methods based on language classification to reconstruct the evolutionary history of partible paternity. Many studies have shown that much cultural variation is well-described by a process of descent with modification in vertically oriented transmission from mother to daughter populations (21–23), whereas others emphasize the importance of horizontal transmission or borrowing of cultural traits from neighboring societies (24–26). Phylogenetic trees based on language have allowed for studies of the evolutionary origins of cultural traits and tests of adaptive hypotheses for other world areas but have not been previously applied to lowland South America.

## Results

**Comparative Database.** Table 2 tabulates data for paternity beliefs and postmarital residence for the major language families in the lowlands. In our comparative sample of 128 societies, partible

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**Table 1. Simple scheme of variation in partible paternity beliefs and extramarital mating**

Increasing partible paternity and extramarital mating	
Singular paternity	Universal partible paternity
Adultery considered immoral	Institutionalized extramarital sex
Violence against adulterous females	Female sexual autonomy
Sex not easily discussed in public	Frequent sexual joking

Extramarital mating is roughly equivalent to what is described as promiscuity in the animal behavior literature and in no way refers to lack of discrimination in female choice but simply the existence of extramarital sexual relationships.

paternity is reported in 53 societies, and singular paternity is reported in 23 societies, leaving 52 societies with unknown conception beliefs. The prevalence of partible paternity across all lowland societies is probably somewhat less than the 70% (53/76) calculated here given that ethnographers may be more likely to report paternity beliefs that are deemed extraordinary and omit mention of singular paternity. Nonetheless, it seems that, in lowland South America, partible paternity beliefs may be more common than the biologically correct version of singular paternity.

In at least six lowland societies, partible paternity is universal in that nearly all offspring have more than one purported father. These societies are the Arawete and Guaja (Tupi-Guarani languages), Canela (Je), Kulina (Arawak), Mehinaku (Arawak), and Matis (Pano), representing four of the five largest language families in the lowlands. Partible paternity beliefs are nearly ubiquitous in Macro-Je (henceforth Je), Pano, Tupi, and Carib language families. Two Carib societies have apparently reverted (see phylogenetic analysis below) to singular paternity (Trio and Kalapalo), and at least five others are probably best characterized with weakly partible paternity. In the Akawaio, Kuikuro, Waiwai, Yekwana, and Yukpa, informants report the theoretical possibility of partible paternity but stress how too much extramarital sex can lead to the birth of undesired twins and/or the general lack of recognition by mothers and secondary fathers. Partible paternity is rare in the Tukano language family (it is only mentioned for Wanano), which is not surprising; this is because Tukanoans are virilocal and men exchange sisters across languages (linguistic exogamy). In smaller language families or unclassified linguistic isolates, paternity beliefs are mixed between partible ( $n = 13$  societies) and singular ( $n = 9$ ) paternity beliefs.

As to postmarital residence, approximately one-half of the societies in our sample are reported to have an uxori-local bias ( $n = 66$ ) and around 30% are virilocal ( $n = 35$ ), with the rest either reported as neolocal or ambilocal ( $n = 25$ ). Treating each society as an independent data point, there is a statistical relationship between paternity beliefs and postmarital residence (Pearson  $\chi^2 = 9.456$ ;  $df = 2$ ;  $P = 0.009$ ), with uxori-locality tending to co-occur with partible paternity. If missing data for partible paternity are treated as singular paternity, the relationship with postmarital residence is

even stronger (Pearson  $\chi^2 = 17.162$ ;  $df = 2$ ;  $P = 0.0002$ ). There are at least four exceptions where partible paternity and virilocality occur together (Table 2). For example, the Panoan Matis is the only society in our sample with virilocal residence and universal partible paternity. Being too stingy with one's genitals is a serious accusation, and both men and women have moral obligations to respond to the sexual advances of a cross cousin (27). Young girls traditionally moved in with future father-in-laws (often mother's brother), who then took part in their sexual development. The Tupi-speaking Cinta Larga, another example of virilocality and partible paternity, traditionally had a preference for men to marry their sister's daughter (28).

Partible paternity is reported in conjunction with virilocality in two other societies. The Wanano practice linguistic exogamy and strict patrilocality like most eastern Tukanoans. Here, extramarital sex outside the patriline is considered grounds for violence against one's wife, whereas there is an emphasis on the solidarity of male kin, often real or classificatory brothers (and likely, cofathers), who communally support all residents of the longhouse (29, 30). However, the Wanano case seems to be exceptional, because other Tukanoans (e.g., Bara, Barasana, Makuna, Taiwano, and Tatuyo) believe in singular paternity. In general, these Tukanoans are very intolerant of extramarital sex and prudish in their everyday talk. Another example similar to the Wanano case is the neighboring Arawak-speaking Curripaco, where brothers share wives in 15% of marriages, sex is not easily discussed in public, extramarital sex is considered immoral, and partible paternity, although certainly a possibility, is generally discouraged except among brothers (31).

**Fitness Benefits of Partible Paternity.** There are several hypotheses for the fitness benefits of partible paternity (Table 3). Although these hypotheses are not exhaustive and are not necessarily mutually exclusive, they do cover a range of likely fitness benefits from both male and female perspectives. Shapiro (32) has argued that partible paternity is simply prostitution or the short-term exchange of fish, meat, and gifts for sex (sex for resources hypothesis). However, we find this unlikely to be a complete explanation given that women also often give gifts to extramarital partners, which suggests competition for some future paternal

**Table 2. Summary of postmarital residence and paternity beliefs divided into the major language families**

Language family	<i>n</i>	Uxorilocal	Virilocal	Ambi/neolocal	Partible paternity	Singular paternity	Unknown beliefs	Partible paternity + virilocal residence
Tupi	23	11	6	5	13	2	8	Cinta Larga
Carib	19	14	1	4	8	2	9	
Je	15	14	0	1	10	0	5	
Pano	10	5	3	2	6	1	3	Matis
Arawak	18	6	9	3	2	4	12	Curripaco
Tukano	8	0	8	0	1	5	2	Wanano
Other	35	16	8	10	13	9	13	
Total	128	66	35	25	53	23	52	4

Cells are counts of ethnolinguistic groups.

**Table 3. Some hypotheses for the benefits of partible paternity from both female and male perspectives, with a prediction for the relationship between cofathers (hostile or amicable) and evidence for and against hypotheses where available**

Hypothesis	Benefits of partible paternity	Cofather relations	Evidence for hypothesis	Evidence against hypothesis
<b>Female strategy</b>				
Resources for sex	Gifts from males for matings	?	Men give meat, fish, and gifts to extramarital partners	Women give gifts to extramarital partners
Multiple investors	Paternal investment from multiple males	?	Higher survival of offspring with other father (Ache and Bari)	
Social benefits	Social bond with other males	?	Women give gifts to extramarital partners	
Gene shopping	Genetic benefits for offspring	Hostile	High-status men have more affairs (Ache and Mehinaku)	
Insurance policy	Insurance if husband dies or defaults	Amicable	Widows marry paramours (Ache, Bari, and Guaja)	Widows do not marry extramarital partners (Canela)
<b>Male strategy</b>				
Sex for resources	Sex and reproduction	?	Men give meat, fish, and gifts to extramarital partners	Women give gifts to men
Mate competition	More extramarital affairs with less risk	Hostile	High-status men have more affairs (Ache and Mehinaku)	
Male alliance	Formalize male alliances	Amicable	Male friends share wives (Arawete, Arara, and Canela)	
Kin bonding	Male kin share wives	Amicable	Brothers share wives (Yanomami, Curripaco, and Wanano)	Cofathers are rarely kin (Ache)
Bet-hedging	Diversify potential paternity and investment	?		

investment (multiple investors hypothesis) and/or development of long-term social ties (social benefits hypothesis). The multiple investors hypothesis, whereby women actively seek paternal investment from multiple men, may account for higher survival rates for Ache and Bari children with one secondary father. The fact that secondary fathers undertake couvade practices in various societies (e.g., Ache, Apinaye, Arawete, Canela, Cashinahua, Krikati, Mehinaku, and Wari) (3, 6, 7, 9–13) also points to publicly recognized, longer-term commitments by other fathers that are consistent with some type of male strategy other than simply sex for resources.

Previous discussions of partible paternity have tended to disregard male interests by emphasizing female control of the mating game (2, 17, 18). This scenario of a female-controlled mating market may indeed characterize many societies. One prediction, as of yet untested, is that cofathers in these contexts are more likely to have adversarial relations, especially if women are gene shopping and men are competing for paternity. The Ache (Tupi-Guarani language), for example, seem to fit this scenario given that primary and secondary fathers tend not to like one another and were traditionally enemies at club fights. However, in many contexts, men have at least some ability to influence the mating market in their favor. One counter adaptation to the high costs of raising someone else's offspring might be to allow (or divert) sexual access of wives to brothers and allies. Under these circumstances, cofathers are likely to maintain more amicable relations. In support of this type of (limited) male control of mating in partible paternity regimens is the common theme of men allowing sexual license to wives among special male friends (e.g., Arara, Arawete, Canela, and Guaja), among real and classificatory brothers (e.g., Curripaco, Matis, Wanano, and Yanomami), and between fathers and sons (Matis).

Of course, some men would benefit from partible paternity if they could secure more matings (mate competition hypothesis). This may often be true for higher-status men that can garner female attention through better gifts, good health, and social capital. Partible paternity beliefs allow these men to father more offspring with more women and fewer repercussions (i.e., lower risk of retaliation or infanticide by jealous husbands). Most

ethnographic studies in the lowlands do not attempt to quantify male social status or relate it to the number of extramarital partners. A notable exception is the study by Gregor (6) of the Arawak-speaking Mehinaku of the Upper Xingu. His data show that the four wealthiest and tallest men [mean = 167.0 cm; 95% bootstrapped confidence interval (CI) = 163.4–173.2 cm] had an average of 7.5 extramarital partners each (CI = 6.3–9.3). Three of them were chiefs and more likely to sponsor and participate in important rituals. The other 11 men in the sample were mostly poor; one man was a chief, whereas the others were nonchiefs or designated into the lowest social stratum known as trash yard men. Their average height was significantly less, averaging 159.4 cm (CI = 156.8–161.7 cm). They had significantly fewer reported extramarital partners, averaging 3.5 each (CI = 2.8–4.4), which was less than one-half the average number reported for high-status men. Other research has shown that better hunters have more extramarital partners and more extramarital children in the Ache (34), and studies generally find positive relationships between hunting ability and mating success (reviewed in ref. 35). Thus, higher-status better hunters and warriors are more likely to be secondary fathers (36, but see ref. 37).

**Phylogenetic Reconstruction.** Given the prevalence of partible paternity beliefs among Je, Carib, Tupi, and Pano speakers across a wide geographic distribution over most of lowland South America, it seems reasonable to posit a deep phylogenetic origin for this mating system. Vertical transmission is a more parsimonious explanation than a diffusion scenario where a wave of institutionalized extramarital sex swept across the lowlands, affecting mostly Je, Carib, Tupi, and Pano languages but not Arawak, Tukano, and around eight smaller language families. We mapped postmarital residence patterns and the presence/absence of partible paternity beliefs onto a phylogenetic tree. Arawak forms an outgroup with Je-Carib-Tupi, according to Rodrigues (38), based on linguistic data and supported by classical genetic markers (39). This is interesting, because the occurrence of virilocality and singular paternity is stronger in Arawak than in Je, Carib, or Tupi language families, perhaps pointing to a phylogenetic origin of uxoricity

and partible paternity at the root of a tentative Je-Carib-Tupi clade (Fig. 1). In other words, previous analyses point to genetic and linguistic evidence that clump Je, Carib, and Tupi language families together, and we can now add cultural evidence (both paternity beliefs and postmarital residence) that also points to similarities in this clade that contrast it with an Arawak outgroup. Other Arawak vs. non-Arawak contrasts are discussed by Hornborg (26). If missing data for partible paternity are treated as singular paternity, then the Arawak base is reconstructed as singular paternity, whereas the reconstruction of the Je-Carib-Tupi base becomes uncertain.

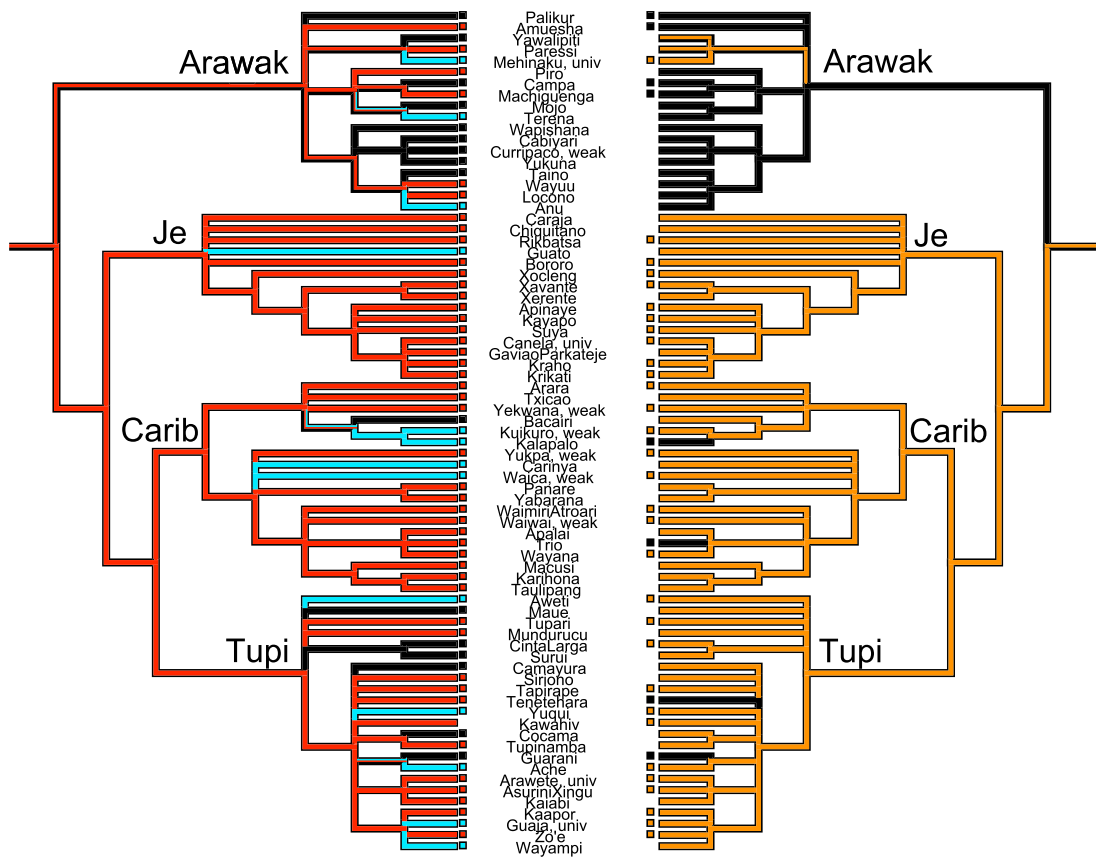
Starting with the assumption that partible paternity likely originated at the Je-Carib-Tupi root, we can estimate the number of evolutionary changes in partible paternity. If the reconstruction is correct, there were two changes from partible to singular paternity in both the Carib and Tupi language families and intensifications to universal partible paternity in Tupi-Guarani (Arawete and Guaja) and Je (Canela). The outgrouping Arawak language family generally tends to more virilocality, perhaps stemming from the Arawak root and consistent with more singular paternity in this language family (four singular and only two partible paternity societies). Removing all missing data and societies with ambilocal/neolocal residence leaves 31 societies with data on partible vs. singular paternity and uxorial vs. virilocal residence. The test by Pagel (40) for correlated discrete character evolution shows positive evidence for evolution between uxorial residence and partible paternity ( $n = 31$ ; difference in log likelihood = 3.0 or approximate Bayes factor of 6). However, this phylogenetic analysis is limited by the fact that we have no way to adjust for

uncertainty inherent in reconstructing the language phylogeny and that we arbitrarily assume equal branch lengths.

### Discussion

Our results point to the widespread geographic and linguistic distribution of partible paternity in lowland South America, especially in Je, Carib, Tupi, Pano, and Arawá language families, that likely stems from a deep history of institutionalized extra-marital mating in the lowlands. Indeed, there is a striking resemblance of partible paternity beliefs across lowland societies, where conception is viewed as a gradual process involving spermous inputs from multiple men. Variations around this theme involve the extent to which women have a role (or not) in the formation of the fetus (e.g., the womb is simply a repository for semen or the woman provides the child's blood), exactly when the conception process begins (e.g., before menarche or after last menstruation), and the amount, if any, of paternal investment by secondary fathers.

We show a correlation between uxorial residence and partible paternity beliefs using both cultures as independent data points and phylogenetic methods. This lends empirical support to the suggestion by Hrdy (17) that women are more likely to mate polyandrously with several men when they have more social power and support from close kin. Alternatively, the strategy of partible paternity may have originated among men (probably high-status men), and then, women began to cluster together with female kin in response to reduced paternal investment from husbands. Uxorial residence and nonexclusive mating relationships are associated cross-culturally with lack of important heritable resources (e.g., land or herds) con-



**Fig. 1.** Postmarital residence (left side: red, uxorial; black, virilocal; cyan, ambi/neolocal) and paternity beliefs (right side: orange, partible; black, singular) mapped onto a phylogeny. Qualifiers are given on some tip names for universal (univ) and weak partible paternity. Both reconstructions use maximum parsimony with 25 evolutionary steps for postmarital residence and 6 steps for paternity beliefs. Language families are labeled at the base of each clade. Branch lengths are arbitrary. Note that missing data exist where societies do not have squares at the tips.

trolled by males (41, 42). Both uxori-local residence and partible paternity seem to have an ancient origin and prevalence in the Je-Carib-Tupi clade and contrast with Tukanoan and Arawak outgroups. The notable exceptions to the rule where partible paternity coexists with virilocality involve young girls moving in with mother's brother, who is either a father-in-law (Matis) or husband (Cinta Larga), and the occasional sharing of paternity within the patrilineal longhouse (Wanano and Curripaco). In these four societies, males might be more tolerant of extramarital relations, because paternity is more likely to be shared with close kin.

Women are likely to actively seek out material benefits and long-term social benefits from extramarital partners. However, in general, men are going to be less likely to invest in a woman and her children if she has relations with other men, even if cofathers are closely related, because investment is better spent on offspring with higher paternity certainty (41). (Mathematically, this is equivalent to children that are mostly their own from a partible paternity perspective.) A man should, however, welcome any investment from other men that increases his wife's fitness along with his own. Therefore, a common result for partible paternity societies is probably low-cost investment by men to extramarital partners that is welcomed or at least, tolerated by husbands. Most lowland societies probably exhibit partible paternity as a female strategy to garner some investment and social support from multiple males. This could be a form of bet-hedging when husbands are likely to desert or die. Men may be able to mitigate the high costs of raising someone else's offspring by exchanging wives with brothers and allies, whereas high-status men manipulate the

extramarital mating market in their favor. We think that the less-to-more extramarital mating scheme in Table 1 is correct but that the underlying processes driving societies to the right or left are multifaceted and include both male and female strategies.

Although our database has provided the few first steps in understanding variation in extramarital mating and conception beliefs across lowland societies, more focused fieldwork is necessary to separate out various hypotheses for the evolution of partible paternity. Based on the limited evidence so far available, we tentatively favor some combination of the multiple investors and social benefits hypotheses as female strategies and the mate competition and male alliance hypotheses as male strategies (Table 3). A number of questions remain unresolved. Does partible paternity correlate with warfare and biased sex ratios? What are the full ramifications of paternity beliefs on social structure and kinship systems, particularly in the potential increase in kin networks by the addition of socially recognized fathers? Most importantly, why is partible paternity rare in the rest of the world and yet, so common in lowland South America? We suspect that the general lack of important heritable resources combined with a strong reliance on kinship and broad networks of social capital in the lowlands have prompted the bargaining and exchange of shared parentage.

### Materials and Methods

The ethnographic sample presented here (Table S1) includes the better-studied indigenous societies residing in the Amazon, Orinoco, and Rio de la Plata river basins. The six most populous language families in lowland South

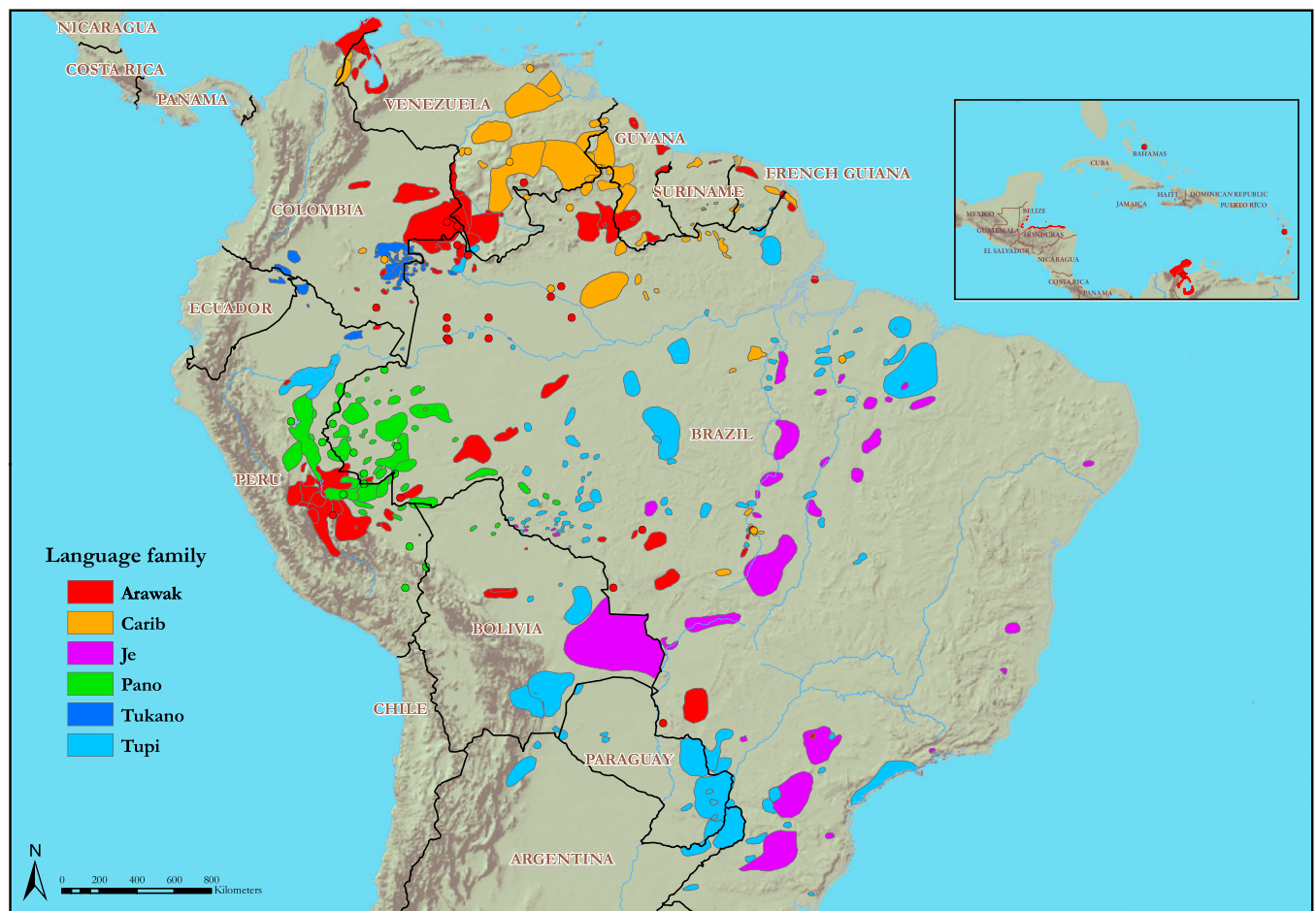


Fig. 2. Approximate distribution of the six major language families discussed in this study. Data provided by World Language Mapping System.

America are the Arawak, Carib, Je, Pano, Tukano, and Tupi (Fig. 2). Tupi is the largest language family, and it is traditionally located mostly south of the Amazon River and on the eastern seaboard. Arawak is the most geographically widespread family of languages, ranging from the mouth of the Amazon to the foothills of the Andes and over 5,000 km from Argentina to the Bahamas. Je is mostly restricted to the Brazilian central highlands. Pano is found mainly in the headwaters of western Amazonian tributaries. Carib is spoken across northeast Amazonia and circum-Caribbean. Tukano languages are found mostly in the upper Rio Negro region. We also included a number of other language families scattered across the lowlands such as the Arawá, Cahuapana, Chapakura, Chibcha, Guahibo, Jivaro, Katukina, Makú, Mataco-Guaicuru, Mosekene, Mura, Nambiquara, Saliva, Tacana, Witoto, Yanomami, Zamuco, and several unclassified isolates.

Data on postmarital residence were first extracted from *Encyclopedia of World Cultures: South America* (43), the corrected ethnographic atlas (44), and the comparative study by Hornborg (45) of 48 lowland societies. Further information on postmarital residence and paternity beliefs (coded as singular or partible with estimated prevalence where available) is from Beckerman and Valentine (2), the Instituto Socioambiental website (<http://pib.socioambiental.org>), and the primary literature (Table S1). In case of

discrepancies in postmarital residence among various sources, we report the majority coding.

Systematic codings of cognates are not available to construct phylogenies for lowland languages (ref. 46 has the current state of Amazonian linguistics). Therefore, we rely on expert classifications (47) of the linguistic relationships among lowland societies. We then use the overall Arawak-Carib-Je-Tupi phylogeny proposed by Rodrigues (38) based on linguistic data and supported by classical genetic markers (38). The genetic data by Salzano et al. (39) reject other linguistic schemes, such as those proposed by Loukotka (48) and Greenberg (49). We use Mesquite software for maximum parsimony reconstructions and the correlated evolution between partible paternity and uxorilocal residence using the linguistic phylogeny (40).

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