

PHYLOGEOGRAPHY, ETHNOBOTANY AND LINGUISTICS: ISSUES ARISING FROM RESEARCH ON THE NATURAL AND CULTURAL HISTORY OF TARO, *COLOCASIA ESCULENTA* (L) SCHOTT

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Ever since the emergence of modern genetics in the early to mid-20th century, there have been scattered attempts to explore the genetic and geographical origins of cultivated taro. There have also been discussions of how local names for the plant in different languages might reflect the origins and movements of cultivated taro. Early cytological studies were consistent with botanical and linguistic evidence indicating that the species originated in Asia, but the question of how to recognise the natural range of taro has always created difficulty. The ability of taro to self-propagate vegetatively, escape from cultivation, and become feral or naturalised, has always been obvious. Less obvious has been the fact that in tropical and subtropical regions, wild taros often flower, fruit, produce seed, and thus have the potential to form breeding populations, whatever the natural or cultural origins may be of each population. Recent ethnobotanical research suggests that the process of naturalisation has been widely encouraged by deliberate planting in suitable natural, modified or cultivated habitats. Under these circumstances, how is it possible to recognise naturally distributed wild types, and thus the natural geographical range within which first use and early or primary domestication might have taken place? Our recent study of chloroplast DNA diversity in taro and closely related species provides a partial solution to the problem, and raises new questions regarding the origins of cultivated taro. Together, recent ethnobotanical, taxonomic, and genetic studies raise questions about what kinds of linguistic data are needed to investigate crop origins and dispersal history. At a broad level of historical analysis, there is good reason to treat linguistic and biological data separately. At the local or ground level, human relationships with plants are mediated through language, so the processes of biological and linguistic change cannot be independent. To understand these processes, and develop more realistic models of crop origins and dispersals, closer integration of linguistic, cultural, and biological research is needed. How people identify plants, use them, and move them about in landscapes is closely related to first-hand physical experience, and to behavioural or cultural traditions that are learned through seeing, doing, and language.

Introduction

In 1956, Jack Rattenbury, inventor of the aceto-carminic staining method for observing chromosomes (Rattenbury 1956a), published a note suggesting that variation in chromosome number and morphology in taro could be used to track human migration across the Pacific (Rattenbury 1956b). This work was followed by surveys of chromosome numbers (Fukushima *et al.* 1962, Kuruvilla and Singh 1981, Yen and Wheeler 1968, Kawahara 1978, Matthews 1984, Zhang and Zhang 1990) and morphology (Coates *et al.* 1988, Parvin *et al.* 2008) in cultivated taro across Asia and the Pacific. As genetic techniques continued to

develop, their application was mostly (but not exclusively) focused on the variation observed in cultivated taro (Lebot and Aradhya 1991, Chen and Zhang 1997, Irwin *et al.* 1998, Tahara *et al.* 1999, Zhu *et al.* 2000, Ochiai *et al.* 2001, Mace and Godwin 2002, Matsuda 2002, Matsuda and Nawata 2002, Yoshino 2002, Kreike *et al.* 2004, Caillon *et al.* 2006, Singh *et al.* 2008, Hu *et al.* 2009, Lebot *et al.* 2010). Restriction fragment length polymorphisms (RFLPs) were easily detected in the non-transcribed spacer (NTS) region of NOR-locus ribosomal DNA (rDNA) and have been useful for distinguishing different wild populations of taro (Matthews and Terauchi 1994, Matthews 2014) and different cultivar groups (Matthews *et al.* 1992, Matsuda 2002, Matsuda and Nawata 2002). Hunt *et al.* (2013) provided the first genetic proof of breeding in a wild population of taro, in Queensland, Australia, by analysing simple sequence repeats (SSRs, also known as ‘microsatellite’ loci) with polymerase chain reaction (PCR) primers designed by previous authors (Mace and Godwin 2002, Hu *et al.* 2009) for work with cultivated taro. Recent but unpublished work on the intergenic transcribed spacer (ITS) regions in rDNA has helped clarify phylogenetic relationships within and between *Colocasia* species (Ahmed 2013).

Most fieldwork for the collection of taro has been conducted for the purposes of cultivar conservation and plant breeding. This has led to a dominance of clonally propagated cultivars in living plant collections, in geographical and genetic surveys of taro, and in estimates of genetic diversity in the species (there has also been a concomitant emphasis on the collection of cultivar-level names for taro, among non-linguists). Many studies have confirmed the presence of cytological and genetic diversity in cultivated taro, but the general lack of sampling of wild populations (whether commensal or natural) has made it inherently difficult to discover the genetic and geographical origins of this crop, and its possible dispersal routes.

In this paper, we outline the logical requirements for identifying the genetic and geographical origins any crop, and subsequent dispersal routes, and for the construction of linguistic records from which historical conclusions can be made. We describe an iterative process of theory building and approximation that is required because of uncertainties inherent in the study of phylogeography. Uncertainties arise from problems in definition (e.g., character-poor descriptions and incomplete species-coverage in plant taxonomy, or the incomplete classification of plant categories defined according to present habitat, genotype, and dispersal history; see Matthews 1996 on plant categories), and problems in observation (e.g., recording bias, inadequate sampling, and sample bias).

A range limit model for the study of crop origins and dispersal

Numerous theories regarding the origins and dispersal of taro have been proposed over many years, by authors concerned with particular aspects of the history of taro. Examples include speculation on the antiquity and origins of taro in the Mediterranean, based on historical and linguistic data (Clusius 1601, Rumphius 2011 [18th C.], de Candolle 1885, Burkill 1938, Matthews 2006), and explanations for the presence or absence of diploid and triploid cultivars in tropical Oceania (Yen and Wheeler 1968), New Zealand (Matthews 1985, 2014), and China (Zhang and Zhang 1990). A more general, theoretical approach was introduced by Matthews (1991):

‘Interpretations of natural range and variation are prerequisites for understanding the selection, propagation and dispersal of taro by humans... If *Colocasia esculenta* (L.) Schott taro originated somewhere as a natural species, and if the geographical range of this species was not extended by humans before its cultivation, then cultivated varieties must have originated within the natural geographical range.’

The second part of this argument begins with a big ‘if’, in which the possibility that taro is *not* a natural species is implicit.

In the following sections, we will discuss taxonomy and phylogeny, geographical range in nature (natural range), geographical range in cultivation (cultivated range), and the definition of plant or population categories relevant for investigating crop history. Each of the following sections will be related to a *range limit model* in which the *hypothetical limits of natural range*, and *range in cultivation*, are represented by two axes that define four geographic quadrats (Figure 1).

Plant populations, however defined, can be placed within the four quadrats according to different scenarios of (a) where the plants originated, and (b) how they dispersed. In this way, the range limit (RL) model is combined with a source-sink (SS) model to create a theoretical framework for collecting and interpreting field observations, taxonomic diversity, genetic diversity, and dispersal history. This framework or phylogeographical model may also be useful for thinking about how names and naming systems for wild and cultivated plants have developed, over space and time.

Taxonomy and phylogeny

The taxonomy of *C. esculenta* (L.) Schott has never been very settled, as the original taxonomic descriptions and the most commonly accepted working

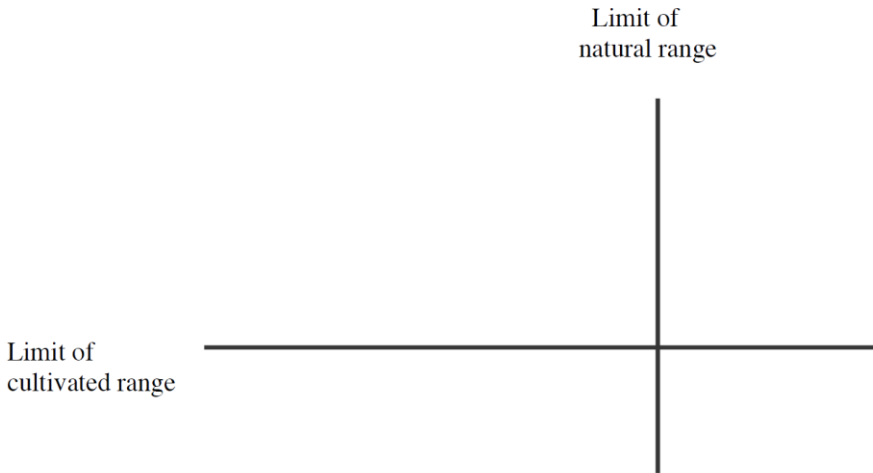


Figure 1: Range limit model for a cultivated species, with geographical range defined by reference to limit of dispersal in cultivation, and limit of natural dispersal. Directionality can be added by reference to the genetic and geographic origins of a species or other taxon of interest (i.e. the phylogeographical starting point) (see Figure 2).

definitions are based largely on variation observed in cultivated varieties. As a cultivated species taro is highly polymorphic (Plucknett 1983, Hay 1998), but revision and description of the species on the basis of wild type plants, from naturally occurring wild populations, is still needed. There is thus no certainty that taro in its cultivated state is in fact a natural species, or that the variation observed is typical of a natural species from which it is derived. High polymorphism in cultivated taro is consistent with the possibility of hybrid origin, which could be a natural origin, or could result from human actions that removed barriers to breeding between closely related, inter-fertile species. High polymorphism in cultivated taro might also reflect diversity in the selection effects of production, utilisation, and propagation while under human management. Diversifying selection, under human management could produce great diversity in visible traits, despite a narrow genetic base (Matthews 2014).

Matthews (1991) noted that an argument for the geographical origin of taro *as a species* can be made by noting where the nearest wild relatives are located:

‘Because all the other species of *Colocasia* are confined to northeast India and Southeast Asia, *C. esculenta* probably originated in this region, as suggested by previous authors for the same reason (Engler and Krause 1920, Hotta 1983).’

The most recent common ancestor of *C. esculenta* and other extant species may have been located in this region. Within the last 20 years, many new species of *Colocasia* have been described (Matthews and Nguyen 2014), and it is now known that wild *Colocasia* species are spread over a much larger area, and mainly in mountains, throughout the wet, northern monsoon region of Asia. Matthews (2014) suggested that the evolutionary origin of taro must be sought over this larger area, and that the lower montane zone may be the most likely area to look, given the eventual spread of taro into tropical lowland regions. For evolutionary studies of *Colocasia* species, it is now clear that analysis of chloroplast genomes can provide a wealth of information (Ahmed *et al.* 2012, Ahmed *et al.* 2013).

In our range limit model (Figure 2), the evolutionary or genetic origin (X) of *C. esculenta* is placed in the vicinity of closely related wild species, inside the present natural and cultivated range of the species. In reality, a species can exist far from other closely related species if environmental changes (e.g. sea level rise, or climate change) lead to geographic disjunction. Evidence for the disjunct distribution of closely-related species would make it more difficult to identify the geographic origin of taro. In fact, all other wild *Colocasia* species are located in Southeast Asia, so it is likely that taro also originated in this region. By definition, the evolutionary origin must lie inside the natural range, and in the case of taro, it can also be placed inside the range of cultivation since taro is cultivated throughout Southeast Asia and beyond.

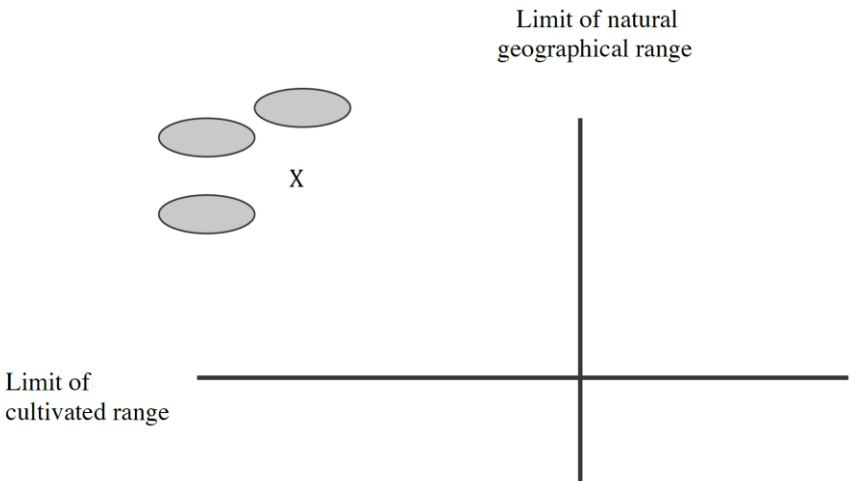


Figure 2: An approximate location (X) for the evolutionary origin of a species is added to the range limit model. Grey areas mark the geographical distributions of closely related wild taxa (e.g. other species of *Colocasia*). *C. esculenta* is thought to have evolved as a natural species in the vicinity of other *Colocasia* species.

Natural range

For taro, the first person to advance an argument on how to recognise the plant as an introduction, rather than as native, or naturally present, may have been de Candolle (1885):

‘The first European navigators saw it in Japan and as far as the north of New Zealand, in consequence probably of an early introduction, and without the certain co-existence of wild stocks.’ (de Candolle 1885:73).

In other words, if ‘wild stocks’ (or natural wild populations) are absent in a given geographical area, then the presence of a cultivated form is most easily explained as the result of human introduction outside the natural range.

In the next sentence, de Candolle also made a key observation that partly explains the presence of wild taro as a commensal plant throughout its cultivated range, in Asia, the Pacific, and other regions:

‘When portions of the stem or of the tuber [i.e. corm] are thrown away by the side of streams, they naturalise themselves easily. This was perhaps the case in Japan and the Fiji Islands, judging from the localities indicated.’ (de Candolle 1885:73).

In cool, temperate regions such as Japan and New Zealand, the introduced and naturalised status of wild taro is easily recognised because temperate climatic conditions (with cool and short summers) make it impossible for the plants to breed (Matthews 1985, 2014). In Fiji, it is likely that climatic conditions permit breeding by wild taros, so naturalisation there might involve seed dispersal. An argument for the necessity of human introduction of taro to Fiji could be made on the basis of the long sea distances that separate Fiji from the continental region of Australia and New Guinea, where wild breeding populations are known. Seed dispersal from the continental region over very long sea distances is improbable for taro, as the seeds are not adapted for wind dispersal (for shorter distances, over land and water, dispersal by fruit-eating birds and mammals is likely).

De Candolle also introduced a linguistic argument linking wildness with the ‘local origin’ of names for the plant:

‘In countries where the species is wild there are common names, sometimes very ancient, totally different from each other, which confirms their local origin. Thus the Sanskrit name is *kuchoo*, which persists in modern Hindu languages – in Bengali for instance.’ (de Candolle 1885:73-74).

Here, de Candolle interpreted diversity in the common names for wild taro as evidence for the local origin of those names and, by implication, for antiquity of the plant to which the names apply (a point he emphasises by noting that

modern Hindu names for taro existed in the ancient Sanskrit language). Others have made the converse argument that the spread of a single name with little variation, across a region and across linguistic boundaries, is evidence for recent introduction of the name, and the plant to which it applies. In the above statement, de Candolle may be using the term ‘wild’ as a casual gloss for the concept of ‘natural’ or ‘indigenous’, or he may be deliberately restricting his argument to the observable contrast of wild and cultivated habitats.

To recognise the natural range of taro, and perhaps any crop, requires various kinds of approximation, field-testing, and further approximation – an iterative research process. Eventually we may reach a useful degree of geographical resolution. As shown above, the first point of reference can be an argument about the natural evolutionary history of the species concerned. After establishing a hypothetical origin, based on previous taxonomic studies and botanical reports of species distribution, the next step is to map wild populations in apparently natural habitats, or habitats that may once have been natural habitats, even if they are now highly disturbed.

In the late 1980s and early 1990s, phenotypically and genetically uniform wild taro populations were found in apparently natural habitats over long distances in tropical rainforest in northeastern Queensland, Australia. This suggested that the natural range of taro extends far from the likely geographical origin of the species, and *outside* the past or present range in cultivation, there being no known early history of taro cultivation in Australia (Matthews 1991, 2014; Yen 1995). This interpretation of natural range is illustrated in an abstract manner in Figure 3, and on a world map by Matthews (2006). Subsequently, the possible northern limits of natural range were then explored in the Ryukyu Islands of southern Japan (Matthews *et al.* 1992), and in the Philippine archipelago (Matthews *et al.* 2012). The possible western limits in the Indian peninsula and Himalaya, and northern limits in China, have not yet been explored.

In the Ryukyu archipelago of southern Japan, the only wild taro present is clearly commensal in its distribution, and lies outside the natural range of the species. In the Philippines, wild taro also appears to be commensal throughout the archipelago. So far, there is no clear association of *C. esculenta* with natural wild habitats in the Philippines. However, a very closely related form of taro, *C. formosana* Hayata, was found in apparently natural wild habitats in northern Luzon (Matthews *et al.* 2009) and the same species is also abundant in Taiwan, in apparently natural habitats (Matthews 2014). Initial genetic data indicates that this species may really be a sub-clade of *C. esculenta* (Ahmed 2013, Ahmed *et al.* 2013), but ecological and genetic studies are needed to confirm this suggestion, before any attempt is made to revise the taxonomy.

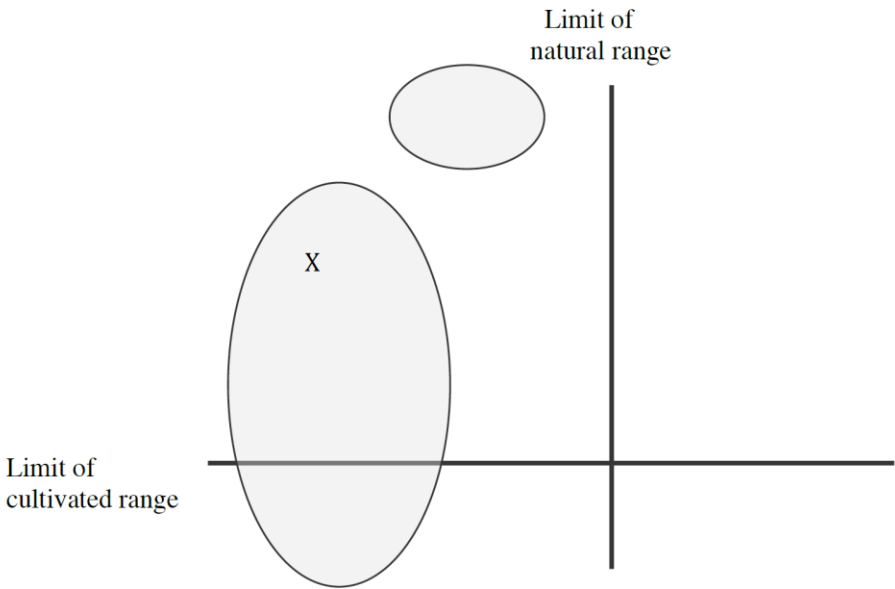


Figure 3: Range limit model, with a wide natural range extending beyond the limit of cultivation, and species origin marked by X (see Figure 2). Natural wild populations (grey ovals) may be continuous or disjunct in their distribution.

Matthews (1995) discussed a range of observations that supported Barrau's (1965) suggestion that progenitors of taro may have resembled var. *aquatilis*, a wild taro variety known from swampy locations in Indonesia. This variety was first described, with illustration, by Rumphius in the late 17th century (Rumphius 2011), and was subsequently collected by Banks and Solander in 1770 in northern Australia (Matthews 2014). The key observations (here expanded) are that this variety is:

- (a) common in the wild (including apparently natural habitats), and displays a general uniformity in appearance (in contrast to the diversity among many commensal and cultivated taros).
- (b) strongly acrid and hence resistant to herbivores, and of limited use to humans (and may be actively removed from gardens when it intrudes),
- (c) diploid and forms wild breeding populations,

(d) associated with insects that have differentiated locally or regionally in specific association with taro. Of particular interest are specialist aroid pollinators (*Colocasiomyia* spp.), the taro grasshopper (*Gesonula* spp.), and the taro plant hopper (*Tarophagus* spp.) (Matthews 1995, Matthews 2003, Matthews *et al.* 2012).

Wild taros conforming in overall vegetative morphology to wild var. *aquatilis* in Indonesia have been observed in Australia, Papua New Guinea, and throughout Southeast Asia, in commensal and also in apparently natural habitats. These vary in acidity and other ways that are not easily observed in rapid field surveys.

Cultivated range

To develop our model for taro, we note that selection, transplantation, cultivation, and other activities involved in domestication must have started somewhere within the natural range of the species. In the absence of any evidence to the contrary, the possible source area for plants in cultivation is the entire natural range, whatever that may be. The possible multiple origins of cultivated taro from different source areas within a wide natural range is illustrated in abstract form in Fig. 4.

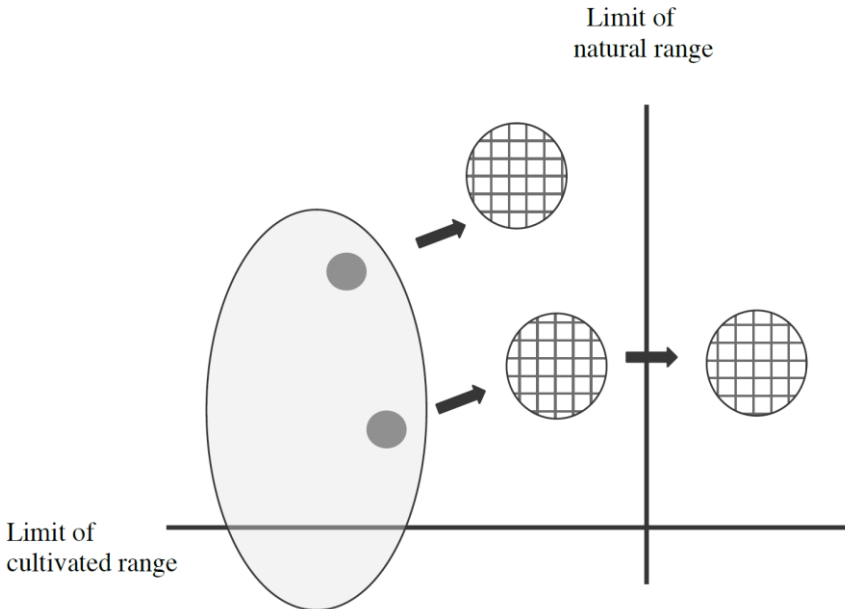


Figure 4: Range limit model showing the possible spread of cultivated populations from multiple source areas (dark circles) within a wide natural range (grey oval). Grid pattern = cultivated population.

When wild and possibly natural populations of taro were found in Papua New Guinea, in the late 1980s, this provided circumstantial support for previous suggestions, based on archaeological evidence, that taro was domesticated early in Papua New Guinea (Matthews 1991, Matthews and Terauchi 1994, Matthews 2014). However, further genetic comparisons between wild and cultivated taros in Papua New Guinea are needed to clarify their relationships.

Cultivated taro could have been introduced to Papua New Guinea early in the agricultural sequence there, if domestication in Southeast Asia was much earlier. In Papua New Guinea, creation of commensal wild populations, genetic mixing with natural wild populations, and human selection might have led to the creation of new cultivars, making the island a center for secondary domestication. The role of commensal wild taro populations in generating genetic diversity is discussed in the next section.

Despite uncertainty in defining the natural range of taro, it is obvious that taro has spread in cultivation far beyond the limits of the likely natural range, from the western Pacific or Near Oceania to Remote Oceania, across the Indian Ocean or through West Asia to Africa and the Mediterranean, and in recent centuries, into North and South America. In tropical to subtropical areas outside the natural range, commensal wild populations created through naturalisation or transplantation into wild habitats may be able to breed. This possibility has not been investigated or reported in equatorial Africa, nor in tropical America or the Caribbean, but flowering and seed production have been reported in a cultivated collection studied in Hawai'i (Whitney *et al.* 1939). When commensal wild taro populations are created in cooler northern or southern latitudes, they can only spread and survive through vegetative self-propagation, or further translocation by humans, as seen in New Zealand (Matthews 1985) and the island of Crete in Greece (Matthews 2006) (cf. Fig. 7, lower right quadrat). Commensal wild populations, inside the natural range, may have had a major role in the domestication of taro, and are discussed further in the next section.

Commensalism and genetic diversity

Combining the range limit model with various source-sink scenarios for wild and cultivated populations forces us to consider how exactly plant populations reproduce, disperse, and become established.

In most studies of crop history, recognising the categories of wild, ruderal, weedy, and cultivated plant populations is generally considered adequate for interpretations of origin and dispersal. Naturalised populations may be regarded as either ruderal (a neutral term that describes the disturbed habitats typically occupied by plants that escape from cultivation), or weedy (if the plants are regarded as a problem for any reason). In the case of taro, naturalised populations are usually assumed to arise through the 'escape' of plants from cultivation, or the discard of unwanted plant parts from food processing areas.

However, they may also be established by direct, deliberate transplantation into the wild. The likely production of fruit and dispersal of seeds by cultivars left to grow in fallow gardens (Matthews 1995) may also contribute to the process.

In some circumstances, common labels such as ‘ruderal’ or ‘weedy’ can be applied to wild taro populations, but ethnobotanical studies suggest that the naturalisation of taro has been widely encouraged by deliberate planting in wet open locations, in and around human settlements, for use as food and pig fodder (Matthews 1985, Matthews *et al.* 1992, Matsuda and Nawata 2002, Matthews and Naing 2005, Matthews *et al.* 2012; see also 17th C. report by Rumphius in early 18th C., Rumphius 2011). The deliberate creation and preservation of commensal wild populations can be called *directed commensalism*. This process can involve transplantation from natural wild populations, other commensal populations, and cultivations into uncultivated (wild) habitats (Figures 5 and 6).

Commensal wild populations might also be derived – in part or whole – from nearby natural wild populations (a process of *de-naturalisation?*), but deliberate planting may be the dominant manner of establishment in regions where wild taro is commonly used as food and fodder (throughout Southeast Asia, and perhaps in other regions too). Once established, commensal wild populations can easily expand by vegetative means (stolon extension and breakage, or break-up of entire clumps on stream or river banks) and seed dispersal. Social regulation of harvesting can ensure that useful wild taro populations are maintained (Matthews 1985, Matthews and Naing 2005, Matthews *et al.* 2012).

In the lower right quadrants of Figures 5 and 6, a commensal wild population is shown outside the natural and cultivated ranges. This could happen without any involvement of cultivated plants (Figure 5), or when a commensal wild taro is introduced directly to a new area without cultivation (Figure 6), but a more likely circumstance may be when the cultivated crop goes out of favour, and is abandoned, at a margin of the cultivated range. Wild commensal populations derived from former cultivations can easily survive in suitably warm and wet habitats, with or without utilisation. Rumphius (2011) noted that an earlier botanist, Clusius (1601), saw ‘African Moors’ looking for the roots and stems of taro near brooks in Portugal and Spain, in order to use them as food, ‘both fried and stewed’. It is possible that by the time of Clusius, taro was no longer much cultivated in the Iberian Peninsula, if at all, and that only the commensal populations remained. It was probably introduced much earlier, in the 8th century A.D., as a cultivated crop during the period of Islamic rule, along with sugarcane (Burkill 1938). In Spain, in the early 11th century, it was recorded as an ornamental plant (Ibn Bassal c. 1080, cited by Harvey 1975), and recently, it has been described as ‘invasive’ (García-de-Lomas *et al.* 2012) (a first report for the plant as invasive, but not for taro *per se*, as the earlier historical records show).

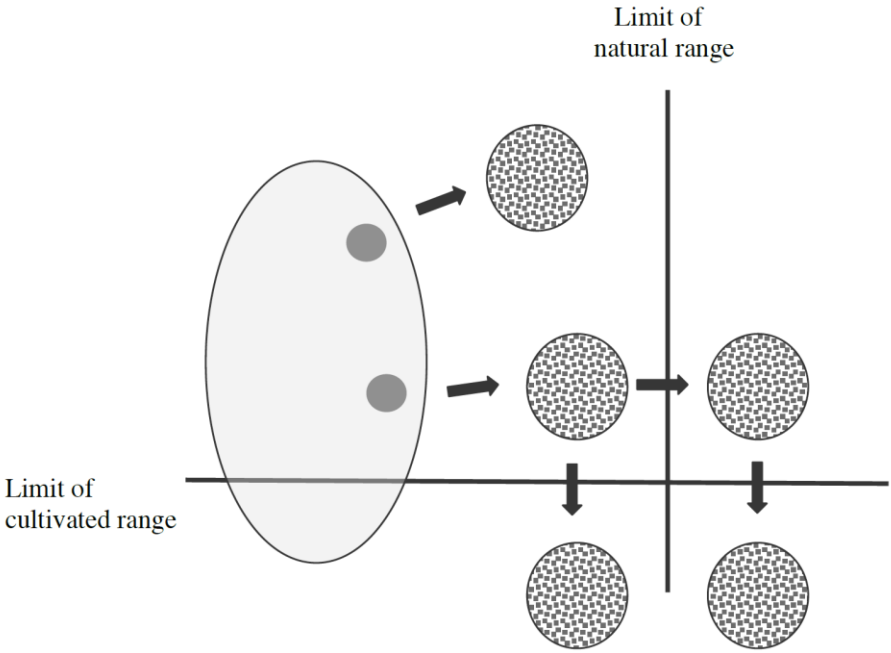


Figure 5: Range limit model showing the establishment and spread of commensal populations (circles with random stipple) from multiple source areas (dark circles) within a wide natural range (grey oval), independently of cultivation. This could be achieved by direct transplantation from one commensal wild population to another, beginning with favoured varieties originating in a polymorphic wild population. To simplify the diagram, arrows are shown as unidirectional. In reality, there can be movements of plants, seeds, and pollen between source and sink populations, in multiple directions.

In northern Australia, wild commensal plants from Southeast Asia may have been introduced directly into springs and streams next to the camps of fishing crews from Southeast Asia, in pre-modern times, thus creating wild commensal populations beyond the cultivated range, but still within the natural range, as shown schematically in the lower-left quadrant of Figure 5. Another possible route, in northern Australia, during the late 19th or early 20th centuries, is via the introduction and then abandonment of cultivars in bush gardens around the temporary camps of migrant rural workers and miners.

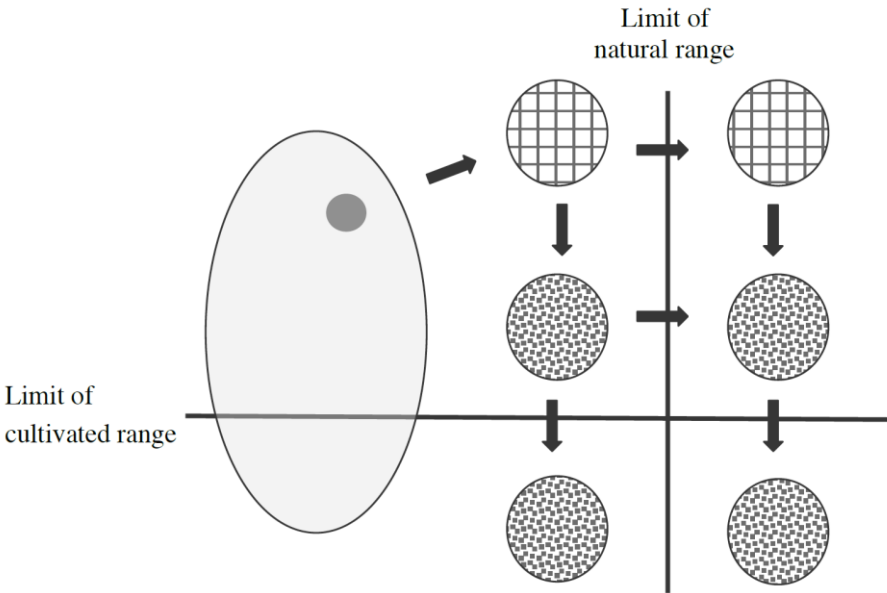


Figure 6: Range limit model showing the establishment and spread of cultivated (grid pattern) and commensal wild (random stipple) populations, from a single source area (dark circle) within a wide natural range (grey oval). In this version of the model, all the commensal wild populations are derived from cultivars. To simplify the diagram, arrows are shown as unidirectional. In reality, there can be movements of plants, seeds, and pollen between source and sink populations, in multiple directions.

The habitat of a commensal wild taro population may be a fragment of natural wild habitat preserved in an otherwise modified landscape (e.g. a stream bank inside a village) or it may be a clearly defined ditch or road bank that is colonised opportunistically by self-propagating plants. The relationship can be called commensal, in a formal ecological sense, because the plants benefit from land, water and nutrient resources that are also used by people, and spread in a more-or-less uncontrolled fashion, without adverse effect for people. The deliberate introduction of useful plants into disturbed or loosely managed wild habitats, in locations near settlements, may have been a basic activity from which many kinds of agriculture have developed, as others have pointed out. It is also an activity that introduces taro into perhaps the least stable of all wild habitats, since human activities often create open habitats by clearing forest, cutting trails and roads, digging ditches, and generally increasing water flow and erosion in the landscape.

In the case of taro, it is proposed here that directed commensalism has led to a vast expansion of wild taro populations of possibly complex origin, throughout Southeast Asia. These populations have expanded in unstable, wet open habitats commonly found inside or near human settlements. Such populations may have become very complex, in genetic terms, if they:

- (a) were derived from diverse cultivated lineages, diverse commensal lineages, and from adjacent natural wild populations that spontaneously colonise the same habitats, and
- (b) occupy unstable environments in which clonal lineages are not able to dominate, so that cross-breeding and reproduction by seed contribute further to their genetic diversity.
- (c) were established in the vicinity of closely-related wild species that are inter-fertile with *C. esculenta*, thus creating opportunities for hybridisation and introgression.

Since commensal populations may also be sources for the selection of new varieties entering cultivation, they may mediate introgression in two directions, from cultivated to natural wild populations, and from natural wild to cultivated populations.

Outside the natural range, commensal taro populations may be less complex, and may be entirely derived from introduced taro varieties that were previously cultivated or commensal. In such situations, if environmental conditions are warm and wet enough for breeding, new cultivars might easily arise from the favoured genotypes introduced, without the influx of unwanted traits (acridity, poor corm qualities, etc.) that are likely to accompany genetic introgression from natural wild forms to domesticated forms of taro. Selection from commensal populations outside the natural range may produce new cultivars efficiently or quickly, but the process is likely to have started more recently than inside the natural range.

Inside the natural range, selection of new cultivars from wild commensal populations may have continued over very long periods, allowing introgression from wild plants into cultivars, despite resistance to unwanted traits.

Refining the search algorithm

In principle, the range limit model proposed here can be used at any taxonomic level to investigate source-sink relationships between wild and cultivated plant (or animal) populations. In our study of taro, we began working at the species taxonomic level, but have discovered multiple genetic sub-lineages within the target species. For each sub-lineage, or intra-specific super-clade, we can establish a new range limit model to help identify geographic and genetic origins, and dispersal routes.

A range limit model for one such lineage, the Type 1 super-clade (Ahmed 2013) is shown in Figure 7. This version of the range limit model represents a refinement of the phylogeographical search algorithm. Through genetic analysis, and wide sampling, we have been able to reduce the phylogeographical search area for the natural origins of tropical, cultivated taro. However, the search area is still very wide, and there are currently no candidate wild populations that can be identified as belonging to the natural range of the IP super-clade.

Models do not generate data, for this we must return to the field, make new observations, and collect new samples for further analysis. The models are merely conceptual tools that help us to see gaps in how information is obtained. For the study of taro, a key gap to address is the location of natural wild populations that display the Type 1 sub-clade of the chloroplast genome (Figure 7).

Many other gaps could also be pointed out, but here we would like to suggest that commensal wild populations are also of key interest. Within the species *C. esculenta* (L.) Schott, such populations may be where the greatest genetic diversity lies, and may be where selection and domestication have been most effective. Although rarely collected and studied, they may have been the main engine for domestication and dispersal of the species. They have been largely ignored in agricultural and taxonomic studies, in anthropological studies of how the plant is managed and used, and in linguistic studies of folk taxonomy.

Over many years, fieldwork has been aimed at locating wild breeding populations of taro, in order to compare such populations with cultivated taro lineages (Matthews 1991, 1997, Hunt *et al.* 2013, Matthews 2014). More strictly speaking, the aim has been to map and describe the *wild descendants* of the *possible wild ancestors* of cultivated taro, and in this way gain insight into the domestication process. Plants living in natural wild populations now may resemble the ancestors of cultivated varieties, but they cannot be the actual ancestors, despite the possibility of clonal lineages surviving for thousands of years.

Taro is known to reproduce by both vegetative and sexual means, tends to be semi-aquatic, and thrives in open wet habitats (Fig. 9). Over time, we can assume that individual clones in wild habitats face the threat of extinction through either canopy overgrowth (forest regeneration), competition with other taro clones, and continuous disturbance (e.g. herbivory, downstream erosion from unstable stream banks, or human reworking of a modified landscape). Natural instability in physical and biotic environments may help to maintain or promote genetic diversity in wild taro populations. In any case, the genetic composition of wild breeding taro populations must be continuously changing at the population level.

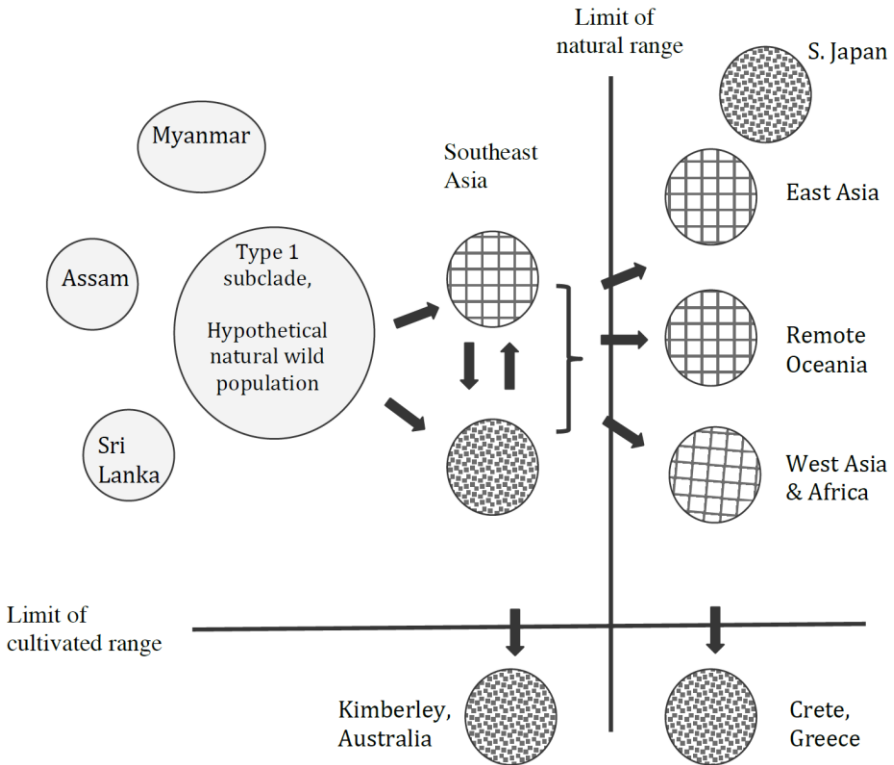


Figure 7: Range limit model applied to the Indo-Pacific (IP) super-clade (Ahmed 2013) of wild and cultivated taro. Grey circles at left (Myanmar, Assam, and Sri Lanka) represent various wild sub-clades of the IP super-clade. The hypothetical natural wild population of the Type 1 sub-clade is likely to be located in the vicinity of these wild sub-clades, near the Bay of Bengal. The Type 1 sub-clade is widespread in SE Asia in commensal wild populations (random stipple) and in cultivation (grid pattern). Beyond the natural range, Type 1 is the dominant chloroplast lineage among tropical cultivated taros. The single Kimberley sample analysed may represent a Type 1 lineage introduced directly as a commensal plant from SE Asia, or in some other manner. Wild taro is present in Crete, but no cultivations are known. The variety is identical in phenotype to cultivars that display Type 1 sub-clade in Cyprus and Egypt. Close interactions between cultivated and wild commensal populations are indicated in SE Asia (see arrows), where breeding is easily observed. Breeding by wild taro has not been seen in southern Japan, and flowers seen in Crete were sterile (Matthews 2006).

In cultivation, the situation is reversed. Long-lived cultivars with outstanding qualities may have been carefully maintained as clones by farmers over

thousands of years – through protection in cultivated habitats, and through proliferation among many farmers over vast distances and in diverse socio-cultural settings.

Regardless of habitat (wild or cultivated), vegetative mutation within clonal lineages ensures that no living plant is genetically identical to the distant ancestor of another living plant. This applies at the whole plant level, and also to the chloroplast genome in particular. Our interest in the chloroplast genome as a focus for genetic analysis follows from early studies (reviewed in Matthews 2014) that showed chloroplast genomes to be both genetically stable but sufficiently variable for evaluating evolutionary relationships among plant species within a genus. Through whole-genome sequence analysis of the taro chloroplast genome, then testing of different *Colocasia* species, and testing of different morphological varieties within *C. esculenta*, we could confirm resolution of genetic variation at the species and subspecies taxonomic levels (Ahmed *et al.* 2012, 2013). This gave us confidence to proceed to a larger survey of samples from within *C. esculenta*, our target species.

Before our survey, at the time of sample collection, and at the time of sample analysis, evolutionary lineages within the chloroplast genomes of taro had not been defined, so our present results have not been biased – with respect to chloroplast genomes – by sample selection. In fact, we used almost all available samples, regardless of their identification as wild or cultivated, or the details of their collection. Our goal was to test samples from as wide a geographical range as possible, and from as many different wild and cultivated sources as possible.

In our recently surveyed sample set, samples identified as ‘wild’ were taken from modified habits typical of commensal populations as well as from apparently natural habitats. Detailed descriptions of habitat, local uses, and local perceptions of the plants were not available for all samples. Over many years, the different collectors contributing to our sample set have used their own criteria for recording plants as wild. The designation as ‘wild’ versus ‘cultivated’ provides very little resolution, in terms of habitat and social context, but the distinction is nevertheless significant for understanding context, and for many samples, further details of context were available.

In future surveys of variation in wild taro, and closely related wild species, special attention should be given to whether or not samples are obtained from:

- (a) commensal populations that are frequently utilised as food or fodder,
- (b) commensal populations that are rarely utilised,
- (c) apparently natural wild populations that are frequently utilised as food or fodder,
- (d) apparently natural wild populations that are rarely utilised.

In most countries where taro is cultivated, it is often assumed, by botanists and agricultural researchers alike, that wild taros are derived by escape from gardens, that they are of low food value or economic value, and that they are not relevant for investigations of the natural flora or investigations of cultivated taro. Even among anthropologists and linguists, the focus of interest in taro has been on cultivated varieties, so that from all perspectives, the wild populations, whether commensal or natural, have been rarely observed, described, or collected. They are under-represented in living collections studied by agricultural institutions, and in herbarium collections that target the natural floras of specific regions. This general bias against recording and collecting wild taro is the main observational bias apparent in previous research on taro.

While escape from gardens is of course a possibility, the vegetative dispersal abilities of cultivars that have been selected primarily for starch production are often less than those of wild taros. The latter are usually harvested in ways that do not interfere with vegetative dispersal, and that may actually encourage such spread. In suitable climates, when harvesting is absent or limited, breeding in commensal wild populations can easily be observed (Fig. 9). If and where such populations are derived from a mixture of cultivated varieties, and receive gene flow from nearby natural wild populations, the local genetic diversity could become very high.

Over long periods of time, commensal populations inside the natural range (see Figure 7) may have been the primary locus for selection and domestication of new varieties that have been taken into cultivation. In commensal wild populations outside the natural range, selection of acceptable or favoured new varieties may be more efficient, without the troubling effects of interaction with natural wild populations. However, such populations are inherently likely to be younger (on average) than commensal populations in settled areas inside the natural range of the species. They are also likely to be derived from a more narrow range of cultivars, being distant from the original sources of variation within the species (i.e. sources inside the natural range).

Implications for linguistic research

In pre-modern times, taro was the most widely distributed starchy food crop in the world, with a distribution ranging from western Africa to northeastern Asia and the eastern Pacific. Its range thus encompassed most language families of Eurasia and the Pacific, including the Austronesian language family. In some cases, the crop may have spread relatively recently among speakers of a particular language family. This must be the case in tropical America, wherever the crop has been adopted by indigenous farmers after its colonial era introduction. In other language families, the taro and its near relatives (Figure 8) may have been known for thousands of years, so determining which language

family has the oldest or first association with taro (*C. esculenta*) may be difficult to determine (cf. Blench 2012).

One way to approach this question is to consider the biological context in which names for taro may have developed, and names associated with wild relatives. In areas where the wild relatives *are not* significant as food plants, their naming may have developed more independently from the naming for taro. In areas where wild relatives *are* significant as food plants, their naming may reflect this significance, and the names may also be more obviously related to names used for cultivated taro.

The utilisation and folk taxonomy of closely related wild aroids has never been investigated in areas where taro, in theory, might have been domesticated. Even if closely related aroids were not involved in the domestication process, their vernacular names might reflect a co-evolution of the naming systems for wild and cultivated aroids. If they were involved in the domestication process, or if they are sufficiently similar in their uses and appearance, the naming systems may be intimately connected.

It is only in the last twenty years that most known wild species of *Colocasia* have been discovered and described by botanists, with the total now being close to twenty (Matthews 2014, Matthews and Nguyen 2014). For most of the newly recognised species, little ethnobotanical research has been carried out. Linguistic records related to wild *Colocasia* species are conspicuously lacking throughout Southeast Asia, even for those that have been known since the 19th or early 20th century.

A range limit model for *Colocasia* species present in Southeast Asia, including *C. esculenta*, is shown in Figure 8. The list of *Colocasia* species indicated in this figure is not complete, but includes most recognised species that are likely to overlap in distribution (i.e., to be sympatric) with wild or cultivated taro. Two species of particular interest, because of their close taxonomic and genetic relationships with *C. esculenta*, are *C. lihengiae* Long and Liu, and *C. formosana* Hayata.

It is predicted that the greatest diversity of names associated with taro (*C. esculenta*) and with the genus (*Colocasia*) will be found where the greatest diversity of species is located (Quadrat 1 in Figure 8). This is because of: (a) the presence of high species diversity, (b) the larger number of plant dispersal categories present within *C. esculenta* (natural wild, commensal wild, and cultivated), and (c) the diversity of language families present in Southeast Asia. However, if most of the wild species are confined to very restricted natural habitats, or have no utility value, or have only become common through very recent expansion of their habitats, they may either lack names, or may have names derived from the better known and more common cultivated species, *C. esculenta*, or other relatively common *Colocasia* species. Many wild aroids are widely known as medicinal plants, including *Colocasia* species, so it is possible

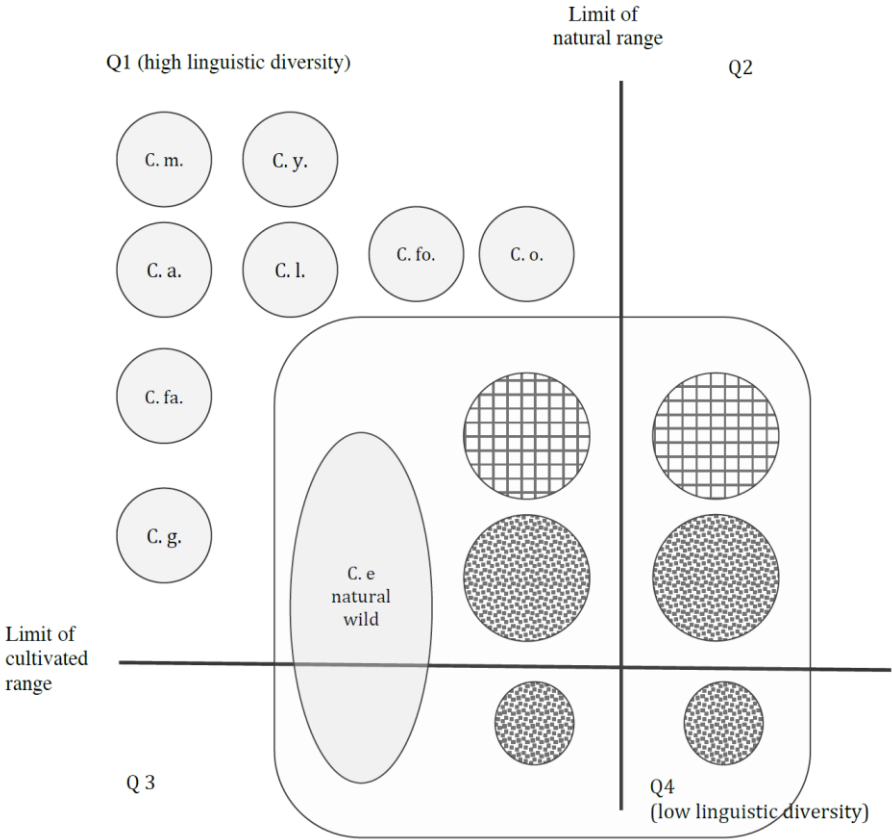


Figure 8: Range limit model for wild *Colocasia* species* known to inhabit low mountain environments close to likely natural range of taro (*C. e.* = *C. esculenta*), in Southeast Asia (Quadrat 1), and taro populations (within large shaded square) identified as natural wild (grey), commensal wild (random stipple), and cultivated (grid pattern). Linguistic diversity associated with taro is predicted to be highest in Q1 (all population categories present), intermediate in Q2 or Q3 (two categories each), and lowest in Q4 (one category). Linguistic diversity in names associated with the genus (*Colocasia*) is predicted to be highest in Q1. * *C. m.* = *C. menglaensis*, *C. y.* = *C. yunnanensis*, *C. a.* = *C. affinis*, *C. l.* = *C. lihengiae*, *C. fo.* = *C. formosana*, *C. o.* = *C. oresbia*, *C. f.* = *C. fallax*, and *C. g.* = *C. gigantea*.

that most wild *Colocasia* species are known to some extent, among people living close to the natural habitats of those species.



Figure 9: Commensal wild taro population on stream bank and in stream (semi-aquatic), next to a permanent spring at the foot of naturally forested limestone hills, East New Britain, Papua New Guinea (Matthews, 9th March 2010). This population was located in a commercial tree plantation and displayed abundant flowering with insect pollinators present. It did not appear to be utilised in any way, and individual plants displayed an apparently wild type morphology (cf. *C. esculenta* var. *aquatilis*). The present open habitat might disappear if a more natural forest is allowed to regenerate in the future.

Certain wild *Colocasia* species may be naturally widespread in Southeast Asia. This appears to be the case with *C. gigantea* (southern China to the Malay Peninsula) and *C. lihengiae* (southern China to Vietnam and northern India). These species do have utility value, and in the case of *C. gigantea*, a domesticated form is also widespread in cultivation, within and beyond the natural range of the species. Names for these two species may be more diverse than those for less utilised wild species, and may or may not be related to names

for taro (*C. esculenta*) in different language families. The name used for one species may be a modification of the name used for another species, and the direction of exchange (if any) may vary in different languages. How names are shared (or not shared) between different species of *Colocasia* may provide important clues for learning about the origins and dispersal of cultivated taro, but will require intensive ethnobotanical and linguistic research, in addition to further field surveys to map the geographical distribution of each botanically recognised species.

Generally, the utilisation of commensal wild taro populations is very different than for cultivated taro (Matthews and Naing 2005, Matthews *et al.* 2012). The former are primarily regarded as a vegetable resource, providing blades, petioles, stolons, and inflorescences for human consumption, and similarly for pigs. The wild plants are usually harvested in a way that allows the population to continue growing *in situ*. Although some taro cultivars are planted for vegetable purposes, the most common aim of cultivation is to produce starchy corms, and this achieved by the selection of varieties that form corms of various size and abundance. To produce corms effectively, leaves cannot be harvested at a young stage, when best for eating, as the photosynthetic work of leaves is essential to the production of corms.

According to how each variety of taro is used, and its status as a wild or cultivated plant, different names may apply to the plant as a whole, to harvested parts, and to the resulting foods presented for eating. Information regarding the use of natural wild taro populations is lacking, but truly wild-type taro is likely to be difficult to prepare and poor for eating, and may therefore be distinguished by names different from those used for commensal wild or cultivated taros. The linguistic diversity in names associated with *C. esculenta* is therefore predicted to be highest where all three categories (natural wild, commensal wild, and cultivated) are present (Fig. 8). The present model is broadly consistent with the diversity reported by Blench (2012) in his survey of names for taro in the Indo-Pacific region.

By recording vernacular names with close attention to how they are used, and to what biological entities they apply, we will have a better chance of discovering the derivation of names according to morphology, habitat, utility, perceived similarities to other aroids, perceived similarities to objects of any kind, known or imagined origins, and symbolic associations.

When, where and how has biological diversity (morphological and genetic) arisen in cultivated and commensal wild populations of taro? Folk taxonomic systems must have developed in response to biological diversity, but must also be involved in how such diversity was generated. When people maintain assemblages of morphologically distinct, named cultivars, the potential for further cultivar diversification (through breeding) is raised. This potential is highest wherever the crop is managed in ways that give plants opportunities to

breed, and people opportunities to find, select, and name new varieties. In the case of taro, such opportunities are likely to be greatest where commensal wild populations exist and are frequently utilised, in close proximity to settlements and rich assemblages of fertile (diploid) cultivars, in physical and biotic environments that are favourable for flowering, pollination, fruiting, seed dispersal, and seedling growth.

Conclusions

The range limit model for the study of crop origins and dispersal may be useful for studies of plant and animal domestication generally. The model accommodates multiple modes of dispersal within and between natural, cultivated, and commensal populations, and requires no assumptions about how plants or animals are dispersed.

To investigate the origins and domestication of taro, the range limit model provides an approximate starting point for analysing genetic and linguistic diversity associated with the crop and its wild relatives. The model can be used to illustrate different scenarios for the origins and dispersal of taro, at different taxonomic levels.

The strong cultural element in past generation of crop diversity and associated names means that our model cannot predict exactly where names are most diverse, or how names originated and dispersed in the phylogeographical regions defined by each quadrat in Figure 7 (a range limit model for sub-clades within a species) and Figure 8 (a range limit model for species within a genus).

The general predictions offered in Figure 8 are testable, and can be used as a starting point for future exploration of names and naming systems associated with taro and its wild relatives (aroid folk taxonomy). Two priority regions for research on aroid genetic diversity and folk taxonomy are around the Bay of Bengal, a large region where tropical taro cultivars may have been first domesticated (Figure 7), and Southeast Asia generally, wherever other *Colocasia* species are found (Figure 8).

Future research on the taxonomy, genetics, ethnobotany, and naming of *Colocasia* species will bring greater resolution to the range limit model, and will raise new questions about particular aspects of the natural and cultural history of taro.

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