Research

Niche construction on Bali: the gods of the countryside

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Human niche construction encompasses both purely biological phenomena, such as the evolution of lactose tolerance, and dual inheritance theory, which investigates the transmission of cultural information. But does niche construction help to explain phenomena in which conscious intention also plays a role? The creation of the engineered landscape of Balinese rice terraces offers a test case. Population genetic analysis and archaeological evidence are used to investigate whether this phenomenon emerged historically from trial and error by generations of farmers, or alternatively was designed by Bali’s rulers. In light of strong support for the former hypothesis, two models are developed to explore the emergence of functional structure at both local and global scales. As time goes forward and selected patterns of irrigation schedules are implemented, local variation in rice harvests influences future decisions by the farmers, creating a coupled human–natural system governed by feedback from the environment. This mathematical analysis received a measure of empirical support when government agricultural policies severed the local feedback channels, resulting in the almost instantaneous collapse of rice harvests. The historical process of niche construction may also have included an evolution of religious consciousness, reflected in the beliefs and practices of the water temple cult.

Keywords: emergence; adaptive agents; evolutionary games; NRY haplotypes; Hegel

1. INTRODUCTION: NICHE CONSTRUCTION IN A COMPLEX SOCIETY

Humans, like beavers and termites, are vigorous practitioners of what biologists call ‘niche construction’: the active modification of their habitat, which can alter selection pressures on behaviour through feedback relationships [1]. Well-known examples include the coevolution of animal domestication and adult tolerance to lactose, and the coevolution of sickle cell anaemia and malaria in response to increasingly settled communities [2,3]. Here, we consider a different process, one that appears to be uniquely human: the deliberate, intentional modification of the natural world. Marx believed that this process defined our species. ‘It is as clear as noon-day,’ he wrote, ‘that man, by his industry, changes the forms of materials furnished by Nature, in such a way as to make them useful to him’ [4]. This process was already so successful in his own time, according to Marx, that nature untouched by human labour had vanished ‘except perhaps on a few Australian coral islands’ [5].

But does the theory of niche construction help us to understand what Marx called ‘humanized nature’? Or is it better suited to cases where there is no question of conscious intention, like lactose tolerance? Here we consider an environment that brings this question into sharp focus. The irrigated rice terraces of the Indonesian island of Bali are among the world’s most productive agroecosystems. A lattice-like structure of canals, tunnels and aqueducts is managed by organized groups of farmers, using specialized networks of ‘water temples’. Is this an example of niche construction? While some scholars argue that the terraced landscape was built by trial and error, others believe that it was created by Balinese kings. The former view may be consistent with niche construction, but the latter is probably not.

Presently, there is little role for conscious planning in the theory of niche construction, which explains the intricate architecture of environments like termite mounds as products of Darwinian selection. But in cases like the rice terraces, the role of conscious intention cannot be ignored. As Marx observed, ‘a spider conducts operations that resemble those of a weaver, and a bee puts to shame many an architect in the construction of her cells. But what distinguishes the worst of architects from the best of bees is this, that the architect raises his structure in imagination before he erects it in reality’ [6]. Current theories of human niche construction, such as dual inheritance, do not directly address this question because they focus on cultural mechanisms of transmission for innovations like dairying or cooking. If human niche construction is to account for historical phenomena like the Balinese case, the analytical focus must be broadened to

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One contribution of 13 to a Theme Issue ‘Human niche construction’.
include the global-scale consequences of conscious innovation as well as the transmission of existing repertoires of cultural information. We return to this point in the discussion.

2. Niche Construction or Royal Engineering?

The first question is whether the rice terraces are indeed an example of niche construction. A long-standing debate about the history of irrigation in Bali bears on this question [7]. Elsewhere in Southeast Asia, the spread of irrigated rice agriculture was usually associated with the expansion of precolonial kingdoms. Typically, the earliest irrigation systems were constructed by villages, and later consolidated and expanded by their rulers [8]. But because of Bali’s steep volcanic topography, ‘the spatial distribution of Balinese irrigation canals, which by their nature cross community boundaries, made it impossible for irrigation to be handled at a purely community level’ [9]. The problem was solved by the creation of a new institution called subak, which began to appear in eleventh century royal inscriptions. Subaks were associations of farmers who managed irrigation water from a common source, such as a spring or irrigation canal. Most ancient irrigation systems encompassed more than one village. For example, an inscription dated AD 1072 refers to a single subak comprising fields located in 27 named hamlets [10].

But the spread of irrigation in Bali was not well documented because Balinese kingdoms never entered an imperial phase, and stopped issuing inscriptions altogether by the middle of the fourteenth century. Half a millennium later, in 1811, Sir Stamford Raffles visited Bali and recorded his surprise that the rajahs of Bali were merely one group of landowners among many others: ‘The sovereign (that is, the Raja of Buleleng) is not here considered the universal landlord; on the contrary, the soil is almost invariably considered as the private property of the subject, in whatever manner it is cultivated or divided’ [11]. The marginal role of Balinese kings in irrigation, also noted by later colonial observers [12], prompted a question that has been debated for nearly a century: Does Bali provide an exception to the thesis that the expansion of irrigation encloses as merely a reservoir of manpower [7,13].

These alternatives can be formalized as follows: one scenario envisions the expansion of irrigation as organized by princes, who mobilized labour to construct irrigation systems in previously forested regions [14]. An alternative ‘budding model’ predicts that the irrigation works were created as a result of local initiatives, with new settlements budding off downstream as a result of population growth. The budding process makes specific predictions about the population genetic structure of the villages, and can therefore be tested through analysis of neutral genetic markers. If the expansion of irrigation was accomplished by the farmers themselves, then population movements of men (patrilineages) would occur as a result of demographic pressure, leading to the formation of new daughter settlements close to parent villages. The budding model would thus predict the formation of small communities located along irrigation systems, with the oldest settlements located at the irrigation outtakes nearest to the most ancient weirs or springs. Alternatively, if large, multi-subak dams were built in virgin territory, there would be no reason for farming communities closest to those dams to be older than those located further downstream.

To evaluate these alternatives, we compared population genetic structure for subaks located in two regions of Bali (figure 1). The first group consisted of 287 farmers who belong to 13 subaks associated with a water temple network in the vicinity of the village of Sebatu, on the upper reaches of the Petanu river. Archaeological evidence suggests that these are among the oldest rice terraces and water temples in Bali [15,16]. The second group consists of 120 farmers belonging to eight subaks located along the Sungi river in the district of Tabanan. The genetic structure of these two groups was compared with the background level of genetic diversity from an additional sample of 100 men, randomly selected from each of the nine geographical regions of Bali.

The results of genetic analyses of these populations are fully explored by Lansing et al. [17,18]; here, we summarize the relevant findings. Subaks located at the furthest positions upstream on their respective irrigation systems on both rivers demonstrate greater levels of genetic differentiation and diversity, suggesting that they came into existence before their downstream neighbours. The budding model predicts decreases in diversity among subpopulations as the process continues in time. Consistent with this prediction, diversity parameters were also higher for the older Sebatu subaks located furthest upstream in their respective irrigation systems than those known to be younger. There was a strong correlation between Y-STR and mitochondrial (mt)DNA structure in the Sebatu subaks ($r = 0.629$). There were also strong correlations between Y-STR variation and geography ($r = 0.541$), and mtDNA and geography ($r = 0.361$), possibly reflecting the same events in population history. No such correlations existed for the Tabanan subaks, or the all-Bali sample (table 1).\footnote{It is worth noting that the budding deme model implies a very restrictive set of constraints on the genetic structure of these farming villages. These include strong founder effects accompanied by genetic drift and directional micro-movements; more structure in patrilineages than in matrilineages; and a strong contrast between subaks versus the background relatedness of the whole population. These are not the expected patterns under the alternative scenario of state-controlled expansion of irrigation; that is, the rajahs encouraging migrations to newly constructed irrigation areas, or alternatively bringing settlers from nearby villages. The evidence from the Y chromosome is consistent with the principal features of the budding deme model: patrilocial residence with very little movement on the landscape, except for occasional micro-movements to nearby daughter settlements.}
The older the subak, the more evidence for this pattern [18].

3. FEEDBACK AND THE EMERGENCE OF FUNCTIONAL STRUCTURE

The genetic evidence is consistent with a process of niche construction pursued by generations of farmers, rather than the execution of a royal blueprint for the expansion of irrigation. But the concept of niche construction implies more than the simple spread of an adaptation. Specifically, niche construction ‘introduces feedback into the evolutionary dynamic... (and) creates an ecological inheritance of modified selection pressures for descendant populations’ [19]. Here we consider whether these two features, evolutionary feedback and ecological inheritance, apply to the Balinese case.

We begin with evolutionary feedback. As noted above, Balinese rice farmers manage their fields collectively in organizations called subaks. Because irrigation depends on seasonal rainfall, each subak’s choice of an irrigation schedule affects the availability of water for their neighbours downstream. The timing of irrigation can also be used to reduce losses caused by rice pests like rats, insects and insect-borne diseases. This is accomplished by synchronizing rice harvests and then briefly flooding the fields, depriving the pests of their habitat. The larger the area that is encompassed by the post-harvest flooding, the fewer the pests. But if too many subaks try to flood their fields at the same time, there will not be enough water. This creates a feedback relationship between the selection of irrigation schedules and the occurrence of water shortages or pest infestations. To explore the effects of this environmental feedback on the behaviour of the farmers, we created two models. The first model explores the effects of feedback on the strategic decisions taken by individual farmers. The second model embeds this logic in an ecological simulation of an entire watershed, and explores feedback effects at a global scale.

The first model consists of a game in which two subaks decide whether or not to synchronize their irrigation schedule [20]. One subak is located upstream of the other, and so controls the flow of water. The subaks can adopt one of two possible cropping patterns, A and B (for example, A could represent planting dates for 1 January and 1 May, while B implies planting on 1 February and 1 June). The water supply is assumed to be adequate for both subaks if they stagger their cropping pattern. But if both plant at the same time, the downstream subak will experience water stress and its harvests will be somewhat reduced. Assume further that pest damage will be higher if plantings are staggered (because the pests can migrate from one field to the next), and lower if plantings are synchronized. Let \( p(0 < p < 1) \) represent the damage caused by the diffusion of pests between the fields, and \( w(0 < w < 1) \) represent the damage caused by water shortage. Given

Table 1. \( F_{ST} \) parameters for Y-SNP haplogroups and mtDNA HVS1 sequences.

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<thead>
<tr>
<th></th>
<th>Y-SNP</th>
<th>mtDNA</th>
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<tr>
<td></td>
<td>( F_{ST} )</td>
<td>( p )</td>
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<tr>
<td>Sebatu subaks (n = 13)</td>
<td>0.141</td>
<td>0</td>
</tr>
<tr>
<td>Tabanan subaks (n = 8)</td>
<td>0.009</td>
<td>0.274</td>
</tr>
<tr>
<td>Bali regions (n = 9)</td>
<td>0.075</td>
<td>0.011</td>
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The older the subak, the more evidence for this pattern [18].

Figure 1. Map of Bali showing locations of Sebatu and Tabanan subaks, and boundaries of the nine districts from which samples were taken. While the older Sebatu subaks are tightly clustered, the Tabanan subaks are spread along the full length of the river. The average geographical distance between the Sebatu subaks is only 3.2 km; it is 13.9 km for those along the Sungi river.
these assumptions, the pay-off matrix is as shown in table 2, where U and D designate the actions of the upstream and downstream subaks, respectively.

In table 2, the first number in each cell is the pay-off for the upstream subak and the second is the pay-off for the downstream subak. For example, if both plant on schedule A, the pay-off for the upstream subak is 1, but it is $1 - w$ for the downstream subak because of insufficient irrigation water.

Several conclusions follow from this simple model. The upstream subaks are never affected by water stress, but their downstream neighbours may be. (This is known to rural sociologists as the ‘tail-ender’ problem: the farmers at the ‘tail end’ of an irrigation system are at the mercy of their neighbours upstream, who control the irrigation flow.) However, the upstream farmers do care about pest damage, because pests, unlike water, can often move upstream. So a strategy of synchronized cropping patterns to control pests will always produce higher yields for the upstream subaks. When $p > w$, the downstream player will also achieve higher yields by synchronizing. Note that if he does so, the aggregate harvest is higher (i.e. the total harvest for both farmers goes up). If $p < w$, the upstream farmer does better by staggered planting, which eliminates his water shortage. Interestingly, adding more pests to the fields until $p > w$ actually increases the aggregate profit for the pair of subaks, because it encourages the upstream farmer to cooperate in a synchronized schedule (even though he must give up some water). But, if the farmers are not worried about pests, the upstream player has no incentive to give up some of his water.

Based on this logic, behaviour in accordance with the model may be predicted. In general, the downstreamers should prefer greater offsets in irrigation schedules, and be willing to accept higher losses from pests as a result, up to $p > w$. The upstreamers, meanwhile, should be willing to give up some of their water to enable the downstreamers to synchronize their irrigation schedule. Both then benefit from a coordinated fallow period, and consequently fewer pests. Put another way, the presence of pests in the ecosystem gives the downstream farmers a bargaining lever they can use to persuade their upstream neighbours to give them the water they need to avoid shortages.

This analysis was subjected to two tests. First, we conducted a survey of 150 farmers in 10 subaks. The results are consistent with the model: upstream farmers tend to worry about pests, while downstream farmers are more concerned about water shortages (table 2). Second, we explored the effects of these choices on the ecological processes defined by the model: irrigation flows and pest damage. To do so, we embedded the decision model in an ecological simulation of rice growth in 172 subaks located along two Balinese rivers, the Oos and Petanu (figure 2). This combined model simulates the effects of decisions about irrigation on the growth of rice and rice pests in the entire watershed. As time goes forward and selected patterns of irrigation schedules are implemented, local variation in rice harvests influences future decisions by the farmers, creating a coupled human–natural system governed by feedback from the environment [22] (table 3).

The 172 subaks that obtain water from the Oos and Petanu rivers are indicated by small squares in figures 2 and 3. At the beginning of each year, the artificial subaks in the model are randomly assigned a schedule of crops to plant for the next 12 months, which defines their irrigation needs. Then, based on historic rainfall data, the model simulates rainfall, river flow, crop growth and pest damage. Rainfall varies by season and elevation, and in combination with groundwater inflow determines river flow. Harvest yields may be reduced by water stress or pest infestations. Pest
population density in each field depends on dispersal from neighbouring fields, as well as growth in situ on locally available food. At the end of the year, harvests are tallied, and each subak selects its cropping schedule for the following year by comparing its harvest with those of $k$ neighbouring subaks, and chooses the schedule that produced the best harvests. Through a process of trial and error, within a few years, subaks form different-sized clusters that share identical cropping patterns. These simulated groupings closely resemble the real clusters of subaks that coordinate their irrigation schedules via the water temple networks (about which more anon).

The rate at which groupings of subaks appear, and their size, is determined by the relative magnitude of $p$ and $r$. Figure 3 shows the effect of increasing $p$, the virulence of pests, on the expansion of synchronized irrigation schedules. If pests are not a factor, there is no need to synchronize harvests, and irrigation schedules are uncoordinated. But when crop losses to pests are high, subaks adapt by synchronizing their irrigation schedules with those of their neighbours, until their losses from water shortages exceed those owing to pests. The result is the aggregation of subaks into different-sized groups with identical cropping patterns. As these groups form, rice harvests improve and variance in harvest yields declines (figure 4).

This model captures an evolving feedback relationship between the decisions of the subaks and the responses of the environment. As shown in figure 3, simple trial and error at the local level produces a patchwork of synchronized irrigation schedules, which over time improves harvests and also reduces variance in harvests. The reduction in variance is potentially significant, because large differences in harvests could discourage cooperation by farmers with suboptimal harvests. These simulated results are supported by responses from farmers to another question in the survey: 97 per cent stated that their own harvest is about the same as that of the other farmers in their subak [23]. Over time, incremental feedback learning becomes consolidated in the social norms of the subak institutions that encourage cooperation among farmers [24].

The formation of different-sized clusters of subaks practising synchronized cropping creates an ecological inheritance of modified selection pressures for descendant populations, and is thus consistent with a process of niche construction. A real-world test of the functional significance of the subak clusters began in the 1970s as an unintended consequence of changes in agricultural policy. At that time, the Asian Development Bank became involved in an effort to boost rice production in Indonesia. The Bank's consultants saw two ways to improve harvests in Bali. The first was to encourage the farmers to grow higher yielding 'Green Revolution' rice varieties, which produce more grain than native Balinese rice. The second recommendation took advantage of another feature of the new rice: it grows faster than native rice. Consequently, the farmers could plant more frequently. The Ministry of Agriculture adopted both recommendations, and competitions were created to reward the farmers who produced the best harvests. By 1977, 70 per cent of the southern Balinese ricebowl was planted with Green Revolution rice, and subaks stopped coordinating their irrigation schedules. At first, rice harvests improved. But a year or two later, Balinese agricultural and irrigation workers began to report 'chaos in water scheduling' and 'explosions of pest populations'. At the time, planners dismissed these occurrences as coincidence, and they urged the farmers to apply higher doses of pesticides, while still competing to grow as much rice per year as possible. This actually intensified both the pest problem [21,25] and water shortages [26]. It was only when farmers spontaneously returned to synchronized planting schemes that harvests began to recover, a point subsequently acknowledged by the final evaluation team from the Asian Development Bank: 'Substitution of the “high technology and bureaucratic” solution in the event proved counter-productive, and was the major factor behind the yield and cropped area declines experienced between 1982 and 1985 .... The cost of the lack of appreciation of the merits of the traditional regime has been high' [21]. Similar results can be achieved by running the simulation model in reverse: beginning the simulation...
Beginning in the late first millennium AD, Balinese rulers established monasteries for both Hindu and Buddhist sects, which originated in India. But the rich mythologies of these foreign religions play virtually no part in the temple rituals, although they are well known to the Balinese from the literature and the performing arts [27]. In contrast to the fully scripted high gods patronized by the rulers, the water temple deities are mere ciphers, usually lacking any attributes beyond their names. Interestingly, in this respect, they resemble the agrarian gods of ancient Rome. The Romans, like the Balinese, imported an entire pantheon of foreign gods, like Zeus, Athena, Dionysius and Hephaestus. But while these deities became the pillars of the state religion, they are largely absent from the Roman countryside. As in Bali, the Roman gods worshipped in the annual calendar of agrarian rites lacked any personality or mode of existence except for instrumental names, which ‘imprisoned them’, as Dumezil observes, ‘in the minor definition of a function, in an act or a fraction of an act, gods like Sarritor (weeding), Occator (harrowing) and Messor (harvesting)’ [28].

Unlike both the Greek and Hindu gods, the imagined capacities of these agrarian temple deities do not exceed their named functions, and their mode of worship consists in the performance of calendrical rites, which provide a ritual template for agricultural labour. In the Balinese temple cult, the colourful and capricious personalities of the foreign gods are backgrounded in favour of the clockwork regularity of the temple rites and irrigation schedules. It is the farmers, rather than the gods, who thus assert control over their engineered landscape. This interpretation is consistent with the views of Cicero, who recognized these gods as personified abstractions: ‘what shall we say of Ops (fortune)? What of Salus (well-being)? Of Concordia, Libertas, Victoria? As each of these things has a power too great to be controlled without a god, it is the thing itself which has received the title of god’ [29].

5. DISCUSSION
Unlike the evolution of lactose tolerance, the construction of the engineered landscape of Balinese rice terraces suggests an expanding role for conscious human agency. Some aspects of this process can be modelled within a Darwinian framework, but others cannot. A Darwinian perspective proved helpful in understanding the choices made by subaks, not because these choices are actually based on mere trial and error, but because they showed that trial and error is sufficient to allow the system to efficiently explore its space of possibilities. In the watershed-scale model, the key to the emergence of global functional structure is the ability of each subak to respond to local ecological feedback involving just two parameters, pests and water. This mathematical analysis might seem suspiciously simple, given the complexity of the Balinese agricultural landscape, but it received a measure of empirical support when government agricultural policies severed the local feedback channels, resulting in the almost instantaneous collapse of rice harvests.

4. SUBAKS AND WATER TEMPLES
In the models described above, the role of conscious intention is limited to the readiness of adaptive agents to seek better harvests by imitating their neighbours. But in reality, more is required. Balinese irrigation systems consist of physically fragile tunnels, canals and aqueducts, which often extend for several kilometres, require constant maintenance and are vulnerable to water theft. While the models provide some insight into the functional structure of this system, they do not account for the high levels of cooperation, planning and social investment that are required to sustain it.

Part of the answer lies in the secular institutions of the subaks. Subaks are self-governing assemblies of farmers, which hold regular meetings and assess fines on members who do not abide by their decisions. However, in surveys, farmers report that punitive fines and sanctions are seldom needed. From their perspective, the most important responsibility of the subaks is the performance of calendrical rites in water temples. By encouraging the farmer’s awareness of their shared dependence on Nature’s bounty, these rites clearly have functional significance. But they also raise a deeper question. Historically, the first references to water temples in royal inscriptions appear soon after the earliest mention of subaks (AD 1071). For example, an inscription provisionally dated to the twelfth century mentions ritual offerings from several subaks in the Sebatu region [18]. If the expansion of subaks and irrigation systems was closely linked to the spread of a specialized cult of water temples, did the process of niche construction encompass a historical evolution of religious consciousness?

One way to approach this question is to ask whether the forms of worship in the water temples have diverged from other practices of Balinese religion.
But a Darwinian perspective is less useful in understanding the principal tool used by the farmers to manage the ecology of the rice terraces: the agricultural calendar. This hybrid instrument grafts a permutable calendar of 10 concurrent weeks, which vary in duration from 1 to 10 days, to the ancient lunar-solar Icaka calendar. The Balinese calendar enables groups of subaks to organize complex interlocking irrigation schedules, composed of varying combinations of water turns and planting schedules, and is the main instrument for irrigation management [21]. Over the centuries, the uses of this calendar have expanded to encompass many other phenomena besides irrigation, including musical notation and cosmology. The historical development of this concept of nested temporal cycles and its successive application to many aspects of the phenomenal world is not well captured by a Darwinian perspective. Instead, it appears to reflect what Hegel described as the desire of Reason to make the world congruent to itself.

Thus, as Hegel observed, the human world is partly made up of ‘objectified ideas’ (buildings, technologies, laws and other products of mental activity). Evolution in the Hegelian sense occurs as the mind encounters its own creations. This process gathers historical momentum as the world appears to become more orderly and comprehensible. In Bali, the concept of nested cycles was extended to personal identity through the adoption of teknonyms (in which a person’s name changes at each step in the life cycle, as they become parents, grandparents and great-grandparents) and birth order names, which cycle from first to fourth born and then repeat (thus the same birth order name is used for the first and fifth born child in a family). Similarly, Balinese literature is full of references to temporal cycles, and the regularity of cyclical progressions is a major theme in Balinese literature. The consistent application of this abstract notion to so many aspects of the Balinese world contributed to a mental and physical landscape of pleasing harmonies and perceptible coherence, in which (to borrow again from Hegel) the workings of Reason appear to pervade the phenomenal world: ‘only then did they feel a real interest in the universe, when they recognized their own Reason in the Reason that pervaded it’ [30].

Should this sort of process be considered in the context of niche construction? We suggest that the answer is yes, if we are to account for phenomena like the engineered landscape of Balinese rice terraces and water temples. ‘In our universe’, writes the molecular biologist François Jacob in a Hegelian vein, ‘matter is arranged in a hierarchy of structures by successive integrations.’ Mind plays no role in the integrations achieved by ordinary Darwinian evolution, but it has tangible effects in human niche construction. Thus, to account for the adoption of innovations like dairying, dual inheritance theory invokes a minimal model of conscious choices. To account for the next hierarchical step—the origin of innovations—requires a less constrained view of mental activity. In Brian Arthur’s view, the growth of technologies is described as an evolutionary process: ‘the collective of technology builds itself from itself with the agency of human inventors and developers much as a coral reef builds itself from the activities of small organisms’ [31]. Something akin to Darwinian selection may be involved, he argues: ‘the many versions of a technology improve in small steps by the selection of better solutions to their internal design problems. But designers also improve technologies by deliberate efforts of their own, and invoking Darwin does not tell us how they do this’.

To explain how technologies undergo what Arthur calls ‘structural deepening’ requires a further step, bringing us closer to Hegel: the active engagement of mind with its own products. Mere tinkering can explain how Balinese farmers engage with their calendars, names, musical compositions or irrigation schedules, but it cannot explain how their world comes to be experienced as a coherent and rational whole. To account for the role of mind at this level, we need to consider the emergence of meaningful patterns in social institutions. An example is Jürgen Habermas’ theory of social learning. Following Hegel, Habermas emphasizes not the end product—the particular congeries of concepts that become dominant in a society—but rather the historical process by which social institutions facilitate or impede the spread of ideas and processes of social learning [32].

The question is, should we attempt to extend the concept of human niche construction to the very summit of Jacob’s hierarchy of integration? Or reserve it for cases that can be made to fit comfortably within a more straightforward biological framework, like dual inheritance theory? To the extent that human niche construction involves mental activity more complex than trial and error, it may become necessary to restore some older philosophers to the pantheon of evolutionary theorists. As the greatest Roman pastoral poet observed, ‘felix qui potuit cognoscere causas . . . fortunatus et ille deos qui nouit agrestis (it is well for one to understand causes . . . fortunate also to comprehend the gods of the countryside)’ [33].

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ENDNOTE

Y-SNP, Y-STR and HVSI are neutral genetic markers used in phylogenetic analysis of genetic samples. Y-SNPs are single nucleotide polymorphisms on the Y chromosome; Y-STRs are short tandem repeats on the Y chromosome; HVSI is a hypervariable region in mtDNA used to track matrilineral ancestry.

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