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Main Manuscript for

Modeling a Primate Technological Niche

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Main Text
Figures 1 to 4

Abstract

Tool transport has been fundamental to the success of our lineage. The relocation of materials from where they naturally occur to where they are needed modifies the environment in a way that increases access to a broader landscape. In contrast, transport of tools over long distances has never been observed in non-human primates. However, chimpanzee stone tools have been recorded farther from their raw material source than what is expected from ethological observations. The mechanisms through which the long-distance relocation of tool material occurs is currently unknown. Here we present an agent-based model, built on observations of wild chimpanzee tool transport that explores the relationship between tool-use, the environment, and the formation of the archaeological record. While our results show that primate tool-use is largely constrained by the environment, there are circumstances in which the aggregated effect of short distance tool transport can dramatically increase the distribution of tool material across a wider landscape. This eventually increases the accessibility of otherwise inaccessible resources over time. Moreover, understanding the landscape patterning that this behavior produces will help us to draw corollaries between tool behavior and its archaeological record. While our results suggest that these processes leave tangible traces in the archaeological record, they are variable and alert us to the disparity between observed behaviors and their archaeological signature.

Significance Statement

Primate tool-use is generally considered to be expedient and largely restricted to places where tool materials and resources occur in close proximity. Our agent-based model shows how the repeated transport of stone tools over short distances can expand where tool-use can occur beyond the natural landscape. These results demonstrate the capacity for chimpanzee technological behavior to modify environments over time. Inferring this behavior from its material record may, however, prove difficult given mismatches between the behavior and its archaeological signature.

Main Text

Introduction

The adaptive success of humans is largely based on the transport of tools to overcome environmental constraints. Over human evolutionary history, this trait has facilitated the expansion of humans and their ancestors across every environment in the terrestrial world (1). The onset of long-distance transport in the Early Stone Age initiated wider access to resources, allowing hominins to exploit a broader landscape (2, 3). This ability to modify the environment through the use and relocation of tool material is considered to be a hallmark of the human niche (3–5). In contrast, stone tool transport in non-human primates is considered to be generally constrained by the environment as tool use only happens when tool materials and food resources occur in the same location and only transport over short distances has been observed (6–9). In the Tai Forest, Côte d'Ivoire, chimpanzee stone hammers have been recorded kilometers from their nearest raw material source (10). However, it is not known whether this form of transport constitutes a modification of the environment that subsequently influences behaviors. Understanding the mechanisms by which chimpanzees move tools over long distances is important as it redistributes tool material across space. This, in turn, may influence tool-using opportunities providing access to resources across a broader landscape (4, 8).

However, daily observations of extant primate stone tool use reflect individual behavior, whereas their landscape scale material record likely represents the aggregation of many tool-using events over multiple years (10). Therefore, understanding how individual bouts of small-scale tool-use produce a landscape scale material signature requires bridging multiple temporal gaps (11). Here we present a spatially explicit agent-based model (ABM), to show that the distance of percussive tools from their sources is a cumulative and emergent property of a system composed of repeated short-distance transport events in a dynamic environment. To this end, we modeled short distance tool transport and use, akin to chimpanzee nut cracking. We vary the location and number of resources – sources of stone and tool-use locations - to further understand the environmental circumstances in which the movement of tools over long distances occur. In doing so, we examine the effect of tool transport on the future opportunities for tool-use and the accessibility of resources over time as well as how such dynamics structure the formation of the primate archaeological record.

These results provide a context in which the landscape scale implications of primate stone tool-use can be discussed. Our model also elucidates the potential role of short distance tool transport in shaping hominin technological landscapes and its material correlates. The tool assemblages generated by the model provide novel an understanding of the dynamic formation of the archaeological record. Such insights are important as there is a growing consensus that primate like tool-use may have been the precursor to the current earliest physical evidence of tool-use and transport in the archaeological record of hominins (12). Yet, there is little understanding of what this record may look like (but see (12)). Behavioral processes such as transport, re-use, and use-life are shown to have a substantial influence on the patterning of the archaeological record (13–15). Therefore, our model, not only provides novel insight into the cumulative effects of short distance tool transport on the broader landscape but also its translation into an archaeological record.

Results

Dynamics between environment and tool-Use. At the beginning of each model run tool-use can only occur in places where a *Tree* is located within 3 grid cells of a *Source*. Simply increasing both the number of *Sources* and/or *Trees* increases the number of places where tool-use is possible (SOM Figure 1: left, Kruskal-Wallis, chi-squared: 225.4, p-value < 2.2e-16). Tool-use occurred at *Trees* located more than 3 grid cells from the nearest source in 95% of the runs. When a *Pounding Tool* is moved from a *Source*, it becomes a secondary source of material for other *Trees*. Provided *Trees* are within three grid cells, tools can be moved beyond a distance of 3 grid cells from their *Source*. As a result, repeated short-distance transport can incrementally move *Pounding Tools* up to a maximum distance of 58 grid cells from their original *Sources*. Consequently, this redistribution of tools increases the number of opportunities for tool-use across a wider landscape. At the end of 88% of all runs, there are more places where tool-use can occur than at the beginning (Figure 2). The runs that did not show an increase in tool-use opportunities are those where the number of *Trees* is initially low (SOM Table 3).

The results of the model show how opportunities for tool-use are impacted by both previously used tools and the density of resources in the environment. *Pounding Tools* move greater maximum distances when *Trees* are more plentiful (Figure 1, Kruskal-Wallis, chi-squared: 1667, p-value < 2.2e-16). The frequency that *Pounding Tools* can be transported and used is regulated by their size and quality. However, the small size of detached fragments in combination with their potentially large size allows Pounding Tools to be utilized 171 to 835 of times prior to exhaustion. While higher quality materials move greater maximum distances (SOM Figure 2), the long use-life of *Pounding Tools* result in a similar spatial distribution regardless of quality.

The interplay between changing *Tree* locations and the extended use-life of *Pounding Tools* further facilitates the incremental distribution of tool materials across the landscape. When the numbers of *Sources* and *Trees* are held constant, iterations where *Trees* die, and new *Trees* appear (i.e. life cycle) during the simulation increases the distance *Pounding Tools* can move from their source (Figure 2, SOM Figures 3, 4). When *Tree* locations remains static, the number of opportunities for tool-use, over time, eventually plateaus and no more loci become available (Figure 2). Conversely, when *Tree* locations are dynamic, opportunities for tool-use do not diminish. Instead, the number of Trees where tool use is possible continues to increase - and would only plateau after all *Trees* in the simulation became available for tool-use - (Figure 2) despite the fact that *Pounding Tool* transport and *Tree* life cycles operate on different temporal scales.

Material Signature. The modeled behavior creates a material record that is comprised predominantly of fragments detached from *Pounding Tools*, but also exhausted and functional *Pounding Tools* in substantially smaller quantities. The spatial distribution, density and composition of the material record is dependent on the environmental circumstances that facilitate the movement of *Pounding Tools*. When *Trees* are infrequent, the resulting assemblages form localized patches in the grid-cells nearest to *Sources* (Figure 3, left). As the number of *Trees* increases, the material record becomes more widespread (Figure 3, middle). *Tree* life cycles have the greatest effect on the distribution of the archaeological record across space (Figure 3, right). These results show that short distance transport, tool-use, coupled with varying resource densities and environmental stability can substantially influence the structure of the archaeological record.

The total amount of discarded material per grid cell, the number of *Pounding Tools* and the mass of *Pounding Tools* form a distance-decay pattern in which these variables are negatively correlated with the distance to *Source* locations (Figures 4, SOM Figure 5). The wide range of variance in these metrics for locations closer to *Sources* is also due to the local configuration of Trees. If the location of *Trees* does not facilitate *Pounding Tool* movement, then tools and their fragments will only occur within the grid cells closest to the *Sources* (Figures 4, SOM Fig. 6, SOM Fig. 7). It is important to note that while this behavior can produce a widespread material record, *Pounding Tools* are not found in every grid-cell that accumulates an assemblage. Environmental circumstances that promote the movement of *Pounding Tools* across space (i.e. numbers of *Trees* or dynamic *Tree* locations) have a negative effect on the proportion of grid-cells that contain tools (Figure 4, SOM Figure 8). In cases, where tools can move large distances, assemblages with *Pounding Tools* comprise as little as 2.5% of the broader material record. This suggests that the archaeological visibility of usable *Pounding Tools* is influenced by the density of *Sources* and resources that require tool-use. This implies that there may be some archaeological assemblages where *Pounding Tools* are infrequent even though the utilization of percussive technology was frequent.

Discussion

The model illustrates the dynamic relationship between short distance tool-use and transport, the environment, and the formation of the archaeological record. Agents only engaged in tool use during chance encounters where tool material could be moved short distances to tool using locations. Though these results show that resources ultimately dictate the opportunities for tool use, in some circumstances, the aggregate effect of this behavior led to the widespread redistribution of tool material across the landscape. Repeated short distance tool transport has the power to move beyond the constraints of the natural environment to increase the number of opportunities for tool use at future time-steps. Moreover, this process can work in tandem with the changing distribution of tool use localities over time to further increase the spread of tool material across the landscape. As a result, the landscape that agents inhabit at time step 0 is markedly different to the one they inhabit at time step 75000.

In regard to primate populations, it has been argued that patterns of tool assisted foraging are largely constrained by encounter rates with resources (8, 9). It has been suggested that long distance movements of tools must occur on rare occasions (6) or that repeated short term transport of tools can result the movement of tools over long distances (16). This, however, has never been observed (10). Here, our model shows that single long distance transport events are not needed to distribute percussive tools across the wider landscape. The aggregate effect of this behavior can increase the number of tool use opportunities over time and space. This illustrates the niche constructing capacity of primate tool using behaviors. The widespread distribution of pounding tools facilitated by their long use-lives generates feedback in which future generations inherit a landscape where opportunities for tool use are greater than they were before. More opportunities for tool-use increases the potential for the acquisition of tool using skills (7, 8). Therefore, short distance tool transport produces a landscape which may ensure the continuation of tool behaviors across generations.

In this light, the results of the model provide a context for exploring how primates modify their landscape beyond the scope of ethological observations. In the Tai Forest, hammerstones have been recorded up to 2 kilometers from the nearest raw material source (10). Furthermore, the distribution of the size and damage intensity of these hammerstones is consistent with the distance-decay relationship described in the model (10). Although short distance transport of tools is observed in the Taï Forest, the broader spatial distribution is the end product of individual behaviors that remain undetected as they mostly happen in the absence of observers. This model illustrates the mechanism by which chimpanzees of the Taï Forest could modify the distribution of tool materials across space through repeated re-use and transport of hammerstones. This may imply that, given that tool use is considered to be socially learned (6), chimpanzees may increase their accessibility to resources through a culturally learned behavior.

Beyond the implications for living primates, researchers have often argued that the capacity to transport material over kilometers at a time was an important aspect of Early Stone Age hominin behavior (2, 3, 17). The results of the model also imply that hominins may have had the capacity to modify their surrounding environment as soon as they began transporting durable materials even short distances at a time. Furthermore, the results of the model also show illustrate how short distance transport, and tool use-life interacts with environmental change. Environmental processes are often argued to be a driving force in hominin evolution (18–21), yet there remains a need to establish links between small scale behavioral processes and long term ecological dynamics(4, 11, 21). Few mechanisms that causally link local scale environmental change to behavior have, however, been purposed or identified (22). Though the behavior of the agents in our model does not change over time, our model illustrates how processes that operate on different temporal scales (i.e. tool use life and environmental stability) can work in tandem to produce feedback that enhances the opportunities for a behavior across time and space. Feedback loops such as the one described here may have influenced opportunities and access of resources to hominins prior to the advent of intentional long-distance transport.

This model provides insights into the translation of a dynamic behavior into the static archaeological record. Within the primate archaeological record, no complete hammerstones have been recovered from archaeological contexts associated with known nut-cracking locations in wild chimpanzees (13). This has been explained by dynamic movement and reuse of stone tools over time leading to an underrepresentation of percussive technology in the archaeological record (13). These results support this notion by showing that environments where tools move more readily across space result in a smaller proportion of assemblages containing pounding tools.

More broadly, the material records generated by the undirected forging strategies of the agents range from localized patches to structured distance decay-patterns. Both of these spatial patterns have been argued as evidence of intentional behavior reflecting planning, foresight, and land use strategies in the hominin record (23, 24). Yet, we show that it is possible to produce both by solely varying the density of resources without changing behavior. Our results emphasize the importance of the interplay between the environment and behavior in structuring the archaeological record (12, 25). In the case of our model, a widespread material record can emerge as a consequence of the interaction between short distance tool transport, tool re-use, use-life, and resource distributions over time. Understanding the mechanisms by which tools are moved and discarded become increasingly critical for interpreting the patterns described in the archaeological record.

Conclusion

This model shows that hammerstone transport over time can have a significant effect on the facilitation of tool behavior itself. The aggregate effect of short transportation events can improve the accessibility of resources within a landscape over time. This landscape pattern of unintentional tool provisioning not only potentially mitigates against local changes in the availability of resources but also increases the opportunity for tool use to be carried out. In this sense, this tool-using behavior provides chimpanzees and potentially other tool-using primates the capacity to positively modify their environments. In the context of living chimpanzee populations, the results of the model in combination with ethological data show that chimpanzees have the potential to incrementally modify their environments through a culturally learned behavior (26, 27).

In sum, our model illustrates how the aggregate effect of short distance transportation events increases the accessibility of resources across a wider landscape over time. Furthermore, the modeled behavior can also interact with changes in landscape structure that promote increases in tool-use opportunities. This highlights the capacity for tool transport to emergently modify environments over the long-term, thus, enhancing the technological niche across generations.

Materials and Methods

The model was designed and implemented using Python 3 and the ABM library Mesa (28). The version of the model present here is actively maintained and available for download by following this link. The model consists of a 250 x 250 grid-cell space that is populated with four types of agents: *Primates*, *Sources*, *Trees*, and *Pounding Tools*. This grid space can be thought of as a forest that agents move through, transporting stone tools over small distances as they encounter resources that require tool-use to access. The tool-use behavior implemented in the model, is designed to approximate Panda nut cracking of Western Chimpanzees (29). *Primates* are agents that can be thought of as chimpanzees who move around the landscape cracking nuts at any opportunity. *Sources* are stationary agents whose locations reflect places where *Pounding Tools* can be acquired (e.g. inselbergs and cobble beds). *Sources* can vary in their "quality" which determines how likely Pounding Tools are to break and lose mass during use.

Pounding Tools are analogous to the hammers used to crack nuts. *Pounding Tools* vary in their mass (grams) and "quality". The size of the *Pounding Tool* is determined by randomly drawing from a normal distribution with mean and standard distribution equivalent to the mass of the stone hammers recovered in the Tai Forest (5). Quality refers to the likelihood a tool will break during use and subsequently lose mass and is determined by the "quality" of the *Source* it is acquired from. *Pounding Tools* can be continuously re-used until they break so much that they are too small (less than 2000 grams) to be used as tools. This size threshold is equivalent to a small Panda nut cracking hammer in the Taï Forest (5).

Trees are agents that represent locations where tool-use can occur. While *Trees* exist only at fixed locations, the redistribution of trees within a forest when tries die and regrow can restructure where the resources are accessible over time (12). To simulate this process, *Trees* increase in age by a unit of 1 after each time-step and will die when their age is equal to 10,000-time steps. When a *Tree's* age reaches 10,000 time-steps tool-use can no longer take place at its location and a new location within a 10 grid-cell radius is randomly chosen as a place for a new *Tree* to "grow." Though the death and growth of *Trees* are not linked in this way in the natural world, this ensures that the number of *Trees* remains constant during the simulation.

When the model is instantiated, *Trees*, *Sources*, and *Primates* are randomly placed within the grid-cell space. Each *Source* is randomly assigned an integer of 0, 25, 50, or 75 representing raw material quality. To prevent every *Tree* from dying at the same time-step, each *Tree* is randomly assigned an age between 1 and 10000. New *Trees* that grow after model initialized begin with an age 0. The population of *Primates* was held constant at 100 for each run of the model. The number of *Sources* is varied between 10, 100, 500. The number of *Trees* varied between 100, 500, 1000, or 2000. The duration of each model run was 75,000 time-steps.

During each time-step, *Primates* move a length of 1 grid cell in a random direction. If the *Primate* moves into a grid-cell that neighbors or is occupied by a *Tree*, the *Primate* will check to see if a *Source* or *Pounding Tool* is within a radius 2 grid-cells around its location. If there is none, then the *Primate* continues to move. If a *Source* is within the search radius of the *Primate*, then the *Primate* will acquire a *Pounding Tool* from this location. If a previously used *Pounding Tool* is found within the search area, then the *Primate* will re-use the *Pounding Tool*. In the event that both *Sources* and *Pounding Tools* are found within the search radius then the *Primate* will choose the *Pounding Tool* or *Source* that is nearest to its location. If multiple *Pounding Tools* or *Sources* are equally near, then the choice is random.

To simulate short distance tool transport and use, the *Primate* moves the acquired *Pounding Tool* to the location of the *Tree* or one of its neighboring grid-cells where it is used and discarded. The likelihood that a *Pounding Tool* will break is determined by a baseline probability of 25% plus its quality. For example, if the quality of the raw material is 25, this is added to the baseline making the break probability for this tool 50%. When a *Pounding Tool* breaks, an additional *Pounding Tool*, representing the fragment, is discarded at the location. The size of the resulting "fragment" is modeled after the observed size distribution of fragments detached from *Pounding Tools* during modern and ancient chimpanzee nut-cracking events in which most breakages result in the production of small fragments but in rare cases fragments can also be large (30).

During the simulation, the model records data about the broader environment as well as each individual *Pounding Tool*. At the global level, the model monitors proximity of live *Trees* to unexhausted *Pounding Tools* and *Sources*. In iterations where *Trees* can die and grow the model also keeps track of the location of the *Trees* through time. In addition, each *Pounding Tool* records the *Source* that it originated from, the number of times it was used for nut-cracking, its initial size and its size after use as well as its location at the end the simulation. At the end of the simulation the model outputs the location of each *Pounding Tool* and any discarded fragments, *Sources*, and *Trees* as well as their attributes. This provides a means to examine the relationship between where tool-use occurs and the location of *Sources* and *Trees* from both systemic and archaeological perspectives.

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Figures and Tables

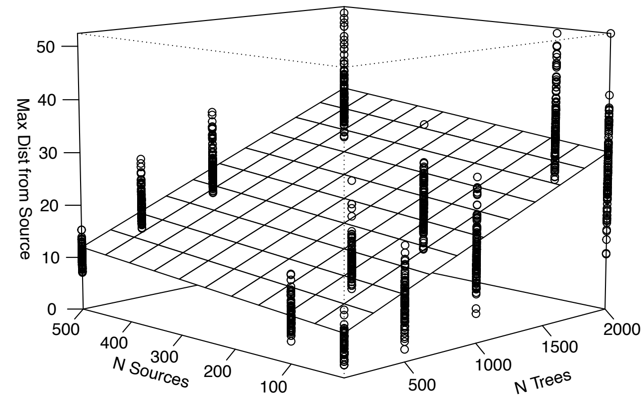

Figure 1. A two-way interaction plot illustrating the effect of the number of *Trees* and number of *Sources* on the maximum distance *Pounding Tools* move from its source. The number of *Sources* has a marginal effect on the maximum distances *Pounding Tools* move but this effect increases with the number of *Trees*. On the other hand, increasing the number of *Trees* has a large effect on the maximum distance a *Pounding Tool* can move from its *Source* (R^2 = 0.77, p = 2.2e-16). The points represent observed values for each iteration for a given parameter combination.

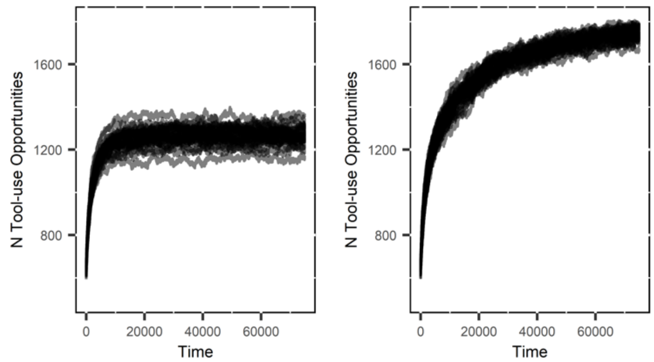

Figure 2. Time-series plots showing the change in the number of Tool-use locations over time in model runs where the number of *Sources* is 500 and the number of *Trees* is 2000. Left: Iterations of the model where the locations of *Trees* remain static throughout the simulation. Right: Iterations of the model where the locations of *Trees* are dynamic. Each line in represents an individual iteration of the model with time represented on the x-axis and the number of tool-use locations represented on the y-axis. Note that in iterations where *Tree* locations are dynamic (right) the number of tool-use locations is always greater. The slope of the lines (right) show that the number of tool-using locations will continue to increase and would eventually plateau only after all 2000 *Trees* became available for tool-use.

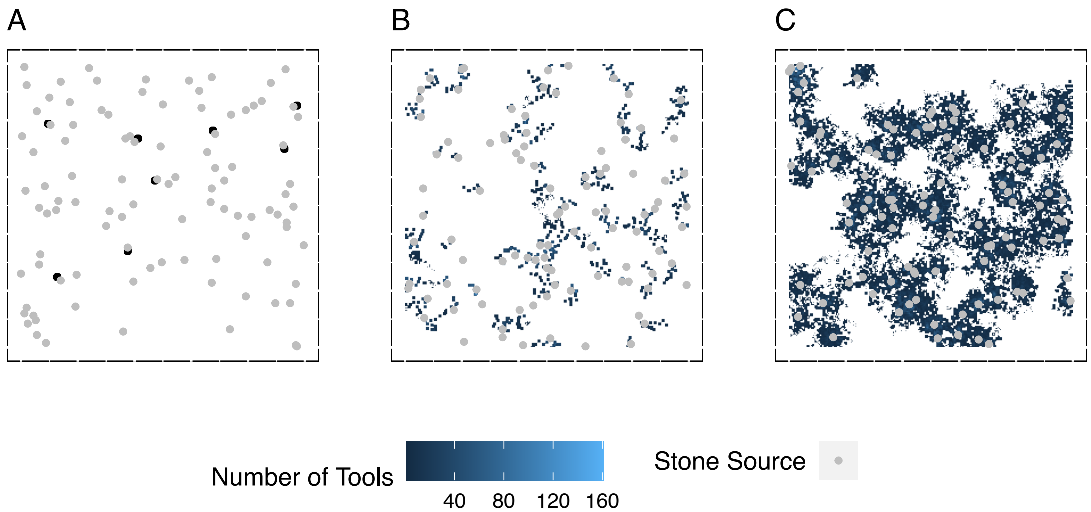

Figure 3. A: The archaeological record when there are 100 *Sources* and 100 *Trees*. Notice that the subsequent archaeological record forms extremely localized patches of material. B: The archaeological record when there are 100 *Sources* and 2000 *Trees*. This archaeological record is becoming more widespread but remains localized. C: The archaeological record when there are 100 *Sources* and 2000 *Trees* where *Tree* locations change over time. Notice how the material record becomes substantially more widespread under these conditions.

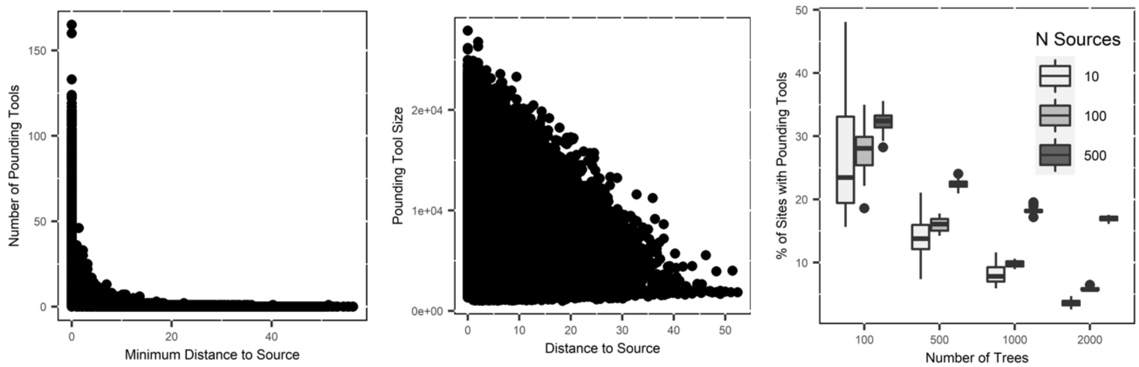

Figure 4. Left: Scatter plot showing the relationship of the number of *Pounding Tools* in a grid cell with the distance to the nearest *source*. Center: The relationship between *Pounding Tool* size and distance to its *Source*. Since grid cells are not associated with a *Source* their relationship to *Sources* is expressed as the minimum distance. Note: All plots show runs where the number of *Sources* is 100 and the number of *Trees* is 2000. See SOM figures 5, 6, and 7 for other model runs. Right: The effect of the environment on the representation of *Pounding tools* in the simulated material record. Increasing the number of *Sources* increases the percentage of assemblages that contain *Pounding Tools*. Increasing the number of *Trees* (See SOM Figure 8) or allowing the *Tree* locations to be dynamic substantially reduces the proportion of assemblages that contain useable tools.