



Essays and Perspectives

Humans as niche constructors: Revisiting the concept of chronic anthropogenic disturbances in ecology



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ABSTRACT

The ecology has witnessed a strong conceptual shift regarding the transition from human-free to human-dominated ecosystems. Nevertheless, human beings are still treated as exogenous factors in many ecological studies. Human activity can reasonably be assumed to influence many processes and patterns studied in ecology at different spatial and temporal scales. Thus, trying to predict the future of ecosystems while ignoring the influence of human activities is neither realistic nor useful. We argue that a successful integration effort in traditional ecology must result from a theoretical and/or conceptual change. A logical and intuitive theoretical leap should be one that considers human actions in light of an integrative scenario. In the first part of this article, we discuss the need for conceptual, theoretical, and methodological changes in studies focusing on the idea of chronic anthropogenic disturbances. In the second part, we introduce the Niche Construction Theory (NCT) as an integrative scenario accommodating these theoretical and conceptual changes in studies that investigate human actions in the environment. To exemplify our argument, we present a case study resulting from our research and focusing on the cascading effects of human activities and their multilevel and multiscale influences in the landscape.

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Introduction

In recent years, the ecology has witnessed a strong conceptual shift regarding the transition from human-free to human-dominated ecosystems. Although an understanding of the implications this transition imposes on biodiversity conservation is not new (Noble and Dirzo, 1997), humans are still treated as exogenous factors, or the anthropogenic influences on ecological process is disregarded in many ecological studies (Liu, 2001). This treatment results in the inevitable questioning of the utility of this traditional approach in ecology. A major change in ecology would thus consist in effectively integrating human activity into ecological research (Alberti et al., 2003).

Most of the terrestrial biomes have been altered by human societies, thus we have generated major pressures on other lifeforms in the planet at a surprising scale, influencing selective pressures and driving the evolution of many species (Alberti et al., 2003; Boivin et al., 2016; Ellis, 2015; Palumbi, 2001). Therefore, the challenge lies in understanding the underlying mechanisms of human behavior that are involved in the interaction between humans and the environment and other species (Liu, 2001). Many processes and patterns studied in ecology are influenced by human activity at different spatial and temporal scales. Consequently, predicting the future of ecosystems while ignoring such activities is neither realistic nor useful.

The adoption of a shift from human-free ecosystems to human-dominated ecosystems (human-altered or human-induced) has apparently been superficial and has not resulted in a real change in ecological practice. We argue that it is imperative to acknowledge the advancements of the archeological and paleoenvironmental

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researches that undermine the pristine ecosystems viewpoint. There are increasing evidences that extensive non-fragmented forest areas or even the deserts are not pristine ecosystems. Instead, prehistoric societies have transformed the ecosystems consistently through domestication processes (including the agriculture and the livestock), soil and water resources management, tree species overexploitation to use as firewood, overhunting and overfishing (Bishop et al., 2015; Colonese et al., 2011; Huebert and Allen, 2016; Neves and Petersen, 2006; Levis et al., 2017; Schmidt et al., 2014; Westaway et al., 2017; Wright, 2017). Therefore, the current composition and the structure of the ecosystems are not determined only by climatic and edaphic factors, but are, in a great extension, influenced by human activities.

When we study a nonhuman species in its habitat, we discuss the “activities” that it performs. By discussing “activities,” we intellectualize the complex interactions between this organism and its environment. In this sense, humans should be considered subjects in ecological experimentation (Alberti et al., 2003). This treatment would enable predicting human behavior and the impact of this behavior on habitats, populations, communities, and ecosystems (Liu, 2001). Otherwise, if there is no paradigm shift, some questions that have motivated researchers for decades will remain unresolved or poorly answered, such as “Why, how, when, where, and to what extent do humans affect other organisms and their abiotic environment? What novel approaches should be developed to answer these questions?” (Liu, 2001).

In this article, we argue that a successful integration effort, starting from traditional ecology, must result from a theoretical and/or conceptual change, and consequently, from changes in the experimental designs of the studies. A logical and intuitive theoretical leap should be one that considers human actions in light of an integrative scenario. Thus, we first discuss conceptual, theoretical, and methodological changes in studies focusing on the concept of “chronic anthropogenic disturbances”. Subsequently, we introduce the Niche Construction Theory (NCT) as an integrative scenario accommodating this theoretical and conceptual change in studies on human actions in the environment.

Chronic anthropogenic disturbances and their relevance for ecology

In forest ecology, the concept of disturbance refers to phenomena that in some way disturbs the stability of a community or an ecosystem. Most of the phenomena considered as disturbances are those caused by the action of climatic or geological factors, such as winds, hurricanes, fires, droughts, rains, frost, snow, floods, earthquakes, landslides, and volcanic eruptions. However, there are also biotic factors considered as disturbances in forest ecosystems, such as outbreaks of plant pathogens, the development of herbivore superpopulations, bioinvasions and human action (Attiwill, 1994). In general, these climatic and geological disturbances are considered inherent processes to ecosystems and shape the composition and structure of forests (Attiwill, 1994).

There is a large set of ecological literature that has investigated the processes by which forest ecosystems can restore themselves after drastic environmental changes caused by human actions such as agriculture, logging, and anthropogenic fires (Costa et al., 2015; D'Oliveira et al., 2013; Francos et al., 2016; García-Orenes et al., 2017; Jang et al., 2016; Mamede and Araújo, 2008; Sobrinho et al., 2016). More recently, ecologists have sought to understand the consequences of more subtle human actions that do not result in drastic and sudden changes in the environment (usually named chronic anthropogenic disturbances; see Singh, 1998), such as wood collection for building houses and

fences or for use as fuelwood, the extractivism of fruits, leaves or tree bark for food, medicinal or commercial purposes, extensive livestock, hunting and fishing (Bhuyan et al., 2003; Hinz et al., 2009; Marinho et al., 2016; Martorell and Peters, 2005; Ribeiro et al., 2015; Ribeiro-Neto et al., 2016; Ureta and Martorell, 2009). Although we believe that other human actions could fit within the scope of the definition of chronic anthropogenic disturbances, we will discuss only the aforementioned actions because they are the ones that literature usually considers and because they are the most widespread uses of forest resources on a global scale.

There are few explicit tests that evidence the ecological consequences of such human actions in the long term. However, some studies about patterns of forest resource uses provide some evidences of such consequences. For instance, wood collection for fuelwood demands large amounts of plant biomass (Medeiros et al., 2011; Ramos et al., 2008; Specht et al., 2015) because it is a resource used daily by low income rural populations from developing countries. Thus, some studies suggest that in the long run this activity may alter species composition (if some species are preferentially used), and decrease the density and total basal area of the tree populations, and consequently decrease the productivity of ecosystems (Lung and Espira, 2015; Rüger et al., 2008; Specht et al., 2015).

On the other hand, the wood collection for houses and fences building has a different dynamic, in which people usually use wood of a few particular tree species whose trunks possess great resistance and durability (Dahdouh-Guebas et al., 2000; Gaugris and Van Rooyen, 2009; Kakudidi, 2007; Medeiros et al., 2011; Nascimento et al., 2009; Oliveira and Hanazaki, 2011). This is because the time of replacement of the wood used on these structures tends to be long (over a decade) (Medeiros et al., 2011). This pattern of selective collection is an indication that, in the long term, this activity may decrease the density of the preferentially used species, leading to changes in the diversity of the local vegetation.

The collection of Non-Timber Forest Products (NTFP) is generally considered to be less harmful to ecosystems because it usually does not lead to the immediate death of the target individuals. However, the excessive collection of fruits and leaves can alter the phenology and fruit yield of the targeted individuals or decrease the recruitment rate, and consequently alter the age structure of the populations (Gaoue and Ticktin, 2007, 2008; Gaoue et al., 2014; Guilherme et al., 2015; Jimoh et al., 2013). In regions where human populations collect tree bark for medicinal or commercial purposes, excessive exploitation of these resources may lead to death of individuals that are mostly intensively collected, which also modifies the age structure and the density of the targeted populations (Feitosa et al., 2014; Ferreira Júnior et al., 2012; Soldati and Albuquerque, 2012). The damage recorded in the reproduction or renewal of the resource targeted for collection has led to the implementation of legal measures that regulate and restrict collections, thus generating conflicts between human societies and the environment.

Moreover, the act of extracting a specific resource, whether wood or another resource, may generate rapid or slow cascading effects on other forest species by changing their life conditions. These changes can result from (a) the formation of trails and forest clearings, which alter microhabitat characteristics such as the amount of light reaching the soil, which can create or eliminate physiological restrictions; (b) people walking in the forest while foraging for resources, thereby inducing unintentional damage and mortality to recently germinated seedlings and saplings; and (c) the sounds produced by people while collecting, which affects the behavior of forest animals (pollinators, dispersers, etc.) (Kissling et al., 2009).

The consequences of livestock grazing on forest or grassland ecosystems are some of the most studied chronic anthropogenic disturbances. There are robust evidences that, over the long term, the overgrazing may result in great changes in the composition of the shrub and herbaceous communities, increasing the dominance of less palatable and grazing resistant species (Cheng et al., 2016; Mudongo et al., 2016). In addition, livestock overgrazing and trampling may hinder the settlement of seedlings and juveniles of tree species (Stewart, 2009). Furthermore, the vegetation cover removal by overgrazing usually results in deterioration of soil physico-chemical characteristics, decrease of macro and micronutrient concentrations, and alteration of the soil microbiota (Albuquerque, 1999; Cheng et al., 2016; Mudongo et al., 2016; Schultz et al., 2011; Schulz et al., 2016; Sousa et al., 2012).

Researchers have recently investigated the chronic anthropogenic disturbances associated with hunting and fishing. Hunting can reduce the population of some species and alter the foraging patterns of target species, possibly impacting other community constituents (Gavin, 2007; Stillfried et al., 2015). Some studies report that bottom fishing has caused changes in the composition and structure of marine benthic fauna. This activity has reduced the biomass of larger benthic organisms and increased the biomass of small benthic organisms, which are presumably less susceptible to the physical disturbance caused by bottom fishing (Hinz et al., 2009; Kaiser et al., 2000).

Some flaws on studies about chronic anthropogenic disturbances and how to solve them

Explicit testing for chronic anthropogenic disturbances has been performed since the 1990s, but to our understanding, most of these studies presented limited conclusions. In this topic, we justify this assertion, bringing evidences that show that the methods that have been applied to estimate the human activities may generate some bias.

One of the first approaches used to study chronic anthropogenic disturbances was the expert-based methods. According to it, researchers subjectively categorize areas as impacted or non-impacted, or rank them in an ordinal disturbance scale and study the structure of plant or animal communities and the ecological processes in these different areas, attributing the variations observed to the different degrees of disturbances (Bojórquez-Tapia et al., 2003; Eggleton et al., 2002; Rawat, 1997). From an operational and practical viewpoint, this approach lacks objectivity and results in constraints to replication by different studies, since the individual experience or the level of knowledge on the vegetation of each researcher can influence the selection and the disposition of the fragments to be studied (Olsen et al., 1999). Moreover, from a theoretical viewpoint, experimental designs that compare human-free to human-disturbed areas (a usual strategy in some ecological studies) overlook the archeological and paleoenvironmental evidences that there are no pristine ecosystems.

Another usual approach is to study the effect of human action on the distribution and abundance of a species or taxonomic group or on a community attribute (for example, by analyzing ecological indices that consider the species richness and composition or their tolerance to human action), and assign the expected results to chronic anthropogenic disturbances. This approach essentially has three flaws (Martorell and Peters, 2005). First, the various types of human activities may affect species or community's attributes differently, and therefore, the choice of a certain type of attribute or species might neglect or overestimate the effects on other species or attributes (Martorell and Peters, 2005). A second limitation is that the use of data from a community attribute or abundance data or distribution of a species as an indicator variable or proxy

of human action, configuring a tautological error because these variables should be used to estimate the consequences of human action (Martorell and Peters, 2005). Third, ecosystems are under the influence of many anthropogenic and non-anthropogenic factors, therefore, trying to estimate different human activities is fundamental to separate what the consequences of each of these activities would be, and what would be the consequences of other factors unrelated to human action.

Some researchers have used geographic information system tools to access long-term changes in the landscape, attributing such changes to human actions considered as chronic disturbances. These studies compare landscape structure variables, particularly variables associated with fragmentation, between the past and current environment, allowing for a great understanding of how historical transformations (highway construction, population increase, urbanization, and logging) have affected local landscapes (Du Toit et al., 2016; Kittredge Junior et al., 2003; Lira et al., 2012; McGarigal et al., 2001). Although methodological advances have been made in remote sensing techniques allowing to assess small-scale changes on landscape (DeVries et al., 2015), this approach does not have the capacity to measure human action on forest resources use, which makes it difficult to predict future changes on ecosystems.

Recently, some researches have used proxy variables as an attempt to estimate the anthropic impact on forest ecosystems. The logic underlying this methodological choice is that these variables are supposed to be correlated with the intensity of forest resources extraction. Examples of these variables include the density and the basal area of trees with evidence of cuttings, number of tree stumps, number and surface area of trails used by people to collect forest resources; proportion of areas used for anthropogenic activities (agriculture, livestock ranching, and urbanization); number of areas with evidence of fire; density of residents in surrounding forest fragments; proximity of forest fragments to human residences, highways, and urban centers; and as proxies of livestock grazing intensity, variables of livestock density, and density or biomass of livestock feces have been used (Leal et al., 2014; Martorell and Peters, 2005, 2009; Martorell et al., 2012; Portilla-Alonso and Martorell, 2011; Ribeiro et al., 2015; Ribeiro-Neto et al., 2016; Rito et al., 2016; Ureta and Martorell, 2009; Villarreal-Barajas and Martorell, 2009). Most of these variables, to our understanding, lack empirical evidence to support their use as proxies for chronic anthropogenic disturbances. Therefore, the findings of these studies may not be demonstrating accurately the consequences of the human actions on the ecosystems.

Although there are evidences that the demographic factors (such as the population density) influence on the demand for forest resources (An et al., 2001; Liu, 2001), using this variable alone does not tell anything about the use of forest resources in an area, and how these potential uses may change the structure of the communities. Thus, the idea of estimating the human actions just by using population density as proxy disregard the likelihood of populations of similar densities to use the forest resources in completely different ways (see Kittredge Junior et al., 2003).

Another potential bias refers to the variables related to forest fragments distance from the urban areas, highways, and human settlements. These variables may be showing consequences of edge effects imposed to the ecosystems during and after these establishments (urbanization, highway construction, and the establishment of human populations) (Chen and Koprowski, 2016; Rotholz and Mandelik, 2013; Vallet et al., 2010). Moreover, another critical weakness of these variables is ignoring the foraging strategies used by people in forest fragments by assuming that people collect forest resources simply by considering distance. The logic in this argument consists in assuming that people adopt an optimization strategy when collecting natural resources, but foragers

also consider the balance between cost (distance, for example) and benefit (quality), which is ignored by these variables. Empirical evidence suggests that people's behavior is frequently suboptimal, i.e., people do not collect forest resources simply depending on distance, and they may cover longer distances to collect high-quality resources or to "escape predators" (inspection by environmental agencies, for example) (Feitosa et al., 2014; Ladio and Lozada, 2000; Smith, 1983; Soldati and Albuquerque, 2012).

Ideally these proxy variables could be replaced or used along with more direct measures of forest resource extraction. Some researchers have undertaken methodological efforts to estimate forest resource consumption (Ramos et al., 2014), but some of these methods are overly laborious and time-consuming. Thus, we suggest that these methods should be adapted using sampling strategies that allow researchers or environmental agencies to measure the consumption of forest resources in a less labor-intensive and time-consuming manner.

For instance, one of the techniques used to measure the consumption of firewood by rural populations is the in situ inventory, according to which the researcher must measure the volume of each branch of wood used in the firewood stocks present in the residences (Ramos et al., 2014). We suggest that this method can be adapted, performing a sampling of the residences, and assessing the approximate volume of firewood stock present in each of the households sampled (Batista and Couto, 2002). Having these data as wood-collecting measures for firewood, researchers can try to map the collection areas, and perform vegetation sampling in these areas, comparing them to areas of different collection intensities. Similar approaches can be used to try to estimate the consequences of other human activities.

Though these methods are laborious, we argue that they could be used along with variables that influence the forest resource use, such as *per capita* income, income from different economic activities, population density, age structure, and degree of education (Babulo et al., 2009; Hegde and Enters, 2000; Kamanga et al., 2009; Lacuna-Richman, 2002; Medeiros et al., 2012; Ramos et al., 2015). Thus, after a reasonable number of studies have been performed, we can choose some proxy variable that we can use more reliably. From that moment on, we can perform modeling studies to try to predict future changes in ecosystems (Pepper et al., 2016, 2017).

With regard to those proxies measures of intensity of livestock grazing (Martorell and Peters, 2005; Ribeiro et al., 2015; Ribeiro-Neto et al., 2016; Schulz et al., 2016), despite seeming less problematic than other variables that attempt to estimate anthropogenic activities indirectly, we argue that the use of these variables requires caution. For example, the type of herd management should be considered, including whether the animals are raised as free range or confined in fenced areas, whether they are free foraging in the ecosystems or are fed fodder (either with native or cultivated flora), and whether the type of grazing is continuous or rotational between different areas. In this case, a practical solution would be performing an experimental design that allows to consider these differences about herd management. Researchers may perform interviews with the local ranchers to understand and register the herd management techniques, and to consider them in the analysis.

Practical solutions to understand the long term consequences of human actions on ecosystems may require a more holistic approach. One of these approaches is long-term social-ecological-focused studies (the focus of disciplines such as ethnobiology, human ecology, and ecological anthropology), which could reduce our limitations to interpreting data. Social-ecological systems result from the dynamic interaction between ecological and sociocultural systems (Berkes and Folke, 1998) and are complex biocultural entities. The intensity of human actions varies over time, and consequently, the ecological parameters measured in the

present may be the result of past actions. For example, studies that have attempted to access people's perceptions about landscape changes in forest ecosystems have observed that previous human actions have a major influence on the current forest structure (Almeida et al., 2016; Katjiua and Ward, 2007; Sieber et al., 2011; Silva et al., 2014).

Currently, we do not know long-term ecological studies that have attempted to estimate the ecological consequences of wood collecting for fuelwood or building houses and fences, or the ecological consequences of fruits and leaves extractivism. However, there are several long-term ecological studies that have observed the consequences of livestock grazing (Cheng et al., 2016; Mudongo et al., 2016; Sousa et al., 2012). The long-term consequences of livestock farming seem to be easier to study compared to other human activities due to the simplicity of establishing control areas (excluding animals by building fences) or because some researchers have taken advantage of logistical opportunities to perform such studies, such as prohibition or abandonment of livestock in areas adjacent to others where this activity is still ongoing, or availing of adjacent areas that have adopted different grazing systems for a long time.

As for other long-term ecological studies that have attempted to address chronic anthropogenic disturbances, there is one study that investigated the effects of tree bark extractivism on *Prunus africana* (Hook f.) Kalkman for ten years (Stewart, 2009). This study observed that in the long term, this activity may lead to a decrease in the density of individuals and a change in population structure toward a reduction in the number of adult individuals and a greater proportion of juvenile individuals in the population, indicating that the tree bark collection may decrease survival of individuals (Stewart, 2009). However, in the last years of sampling the studied population, the occurrence of fires and livestock grazing may have had some influence on the observed final results.

Human as niche constructors: a change in perspective for ecology

From our perspective, a scenario that allows for a theoretical, heuristic, and methodological approach to understand the consequences of human activities on ecosystems is the Niche Construction Theory (NCT). The NCT is based on the premise that all the organisms have the ability to change (deliberately or not) the environmental conditions in their surroundings in a significant manner in space and time to the point where they modify the selective pressures acting on themselves and other organisms, with consequent evolutionary implications (Odling-Smee et al., 2003).

The NCT does not acknowledge the humans' actions just as disturbance, but acknowledges that the extensive environmental alterations by humans change the selective pressures that act on other species, including non-domesticated species. There are many recent evidences about this process, such as decreasing on lizards limbs living near urban areas allowing a more efficient moving, morphological changes on wings birds species allowing them to fly to more distant areas among forest fragments, changes on body height or body biomass on fish and shellfish species due the overfishing on larger individuals, and phenological changes on plant species due climatic changes (Alberti et al., 2016; El Yaacoubi et al., 2014; Sullivan et al., 2017). These phenomena cannot be explained by just considering the human actions as disturbances.

The forest resource extraction may have similar consequences. As we already mentioned, people have criteria to choose what plant species or individual they will collect. This behavior may generate selective pressures on plant species. In some situations, the selective collection of individuals with an intended phenotype may decrease the ratio of individuals with this phenotype in the long term. It has been noticed on two plant species harvested

as medicinal, the American ginseng (*Panax quinquefolius* L) and Himalayan snow lotus (*Saussurea laniceps* Hand.-Mazz) (Law and Salick, 2005; McGraw, 2001). There are evidences that people usually collect the larger individuals from these species. Thus, both of them presented decreases in their length in areas of intensive extractivism throughout the 20th century.

But, there are situations in which the anthropogenic management may increase the ratio of the intended phenotype. Throughout its evolutionary history, humans have deliberately managed edible plants with the aim to increase their productivity, or decrease the concentration of harmful compounds (Meyer et al., 2015; Ramos-Madriral et al., 2016; Sullivan et al., 2017). This phenomenon has also been identified in plant species through incipient domestication process. Ethnobiological studies have demonstrated that plant individuals in areas more anthropogenically managed present morphological characteristics (such as fruits and seeds size and biomass) preferred by the people than the individuals occurring in areas less anthropogenically managed (Casas and Caballero, 1996; Sousa Júnior et al., 2016).

Undoubtedly, the interaction among species (including humans) is one of the most important factors in understanding the distribution and abundance of species in ecosystems. Nevertheless, we argue it is imperative extrapolating the well-studied predation and competition relations. Some species have a great potential to change the flow of matter and energy on the ecosystems (phenomenon named ecosystems engineering). Ecological studies have demonstrated many examples of ecosystems engineers, such as the potential of earthworms on changing the physical structure and the productivity of soils, the physicochemical changes on mangrove soils produced by crabs, or the microclimatic changes created by the establishment of trees species in a forest (Gutierrez and Jones, 2006; Jones et al., 1994, 1997). These alterations promoted by some species can change or create habitats and environmental pressures that can influence their and the other affected species evolution (Odling-Smee et al., 2003).

However, two criteria are fundamental to identify the existence of niche construction (Matthews et al., 2014). The first criterion is the ability of a given organism to substantially modify the environmental conditions (biotic and abiotic) of its surroundings. The second criterion is that the environmental changes promoted by the organism should be sufficient to change or create new selective pressures that result in evolutionary consequences acting on the niche constructor itself or on other organisms (receptors). Thus, the occurrence of ecosystem engineering alone is not enough to generate the niche construction.

For an evolutionary impact from niche construction to exist, an evolutionary response in receptor organisms that originated from an environmental change caused by the constructor organism is necessary (Matthews et al., 2014). Thus, the NCT adopts a broad concept of evolution, introducing the “ecological inheritance” concept as an evolutionary process that is as relevant as genetic inheritance (Odling-Smee et al., 2013). We will further explain this idea based on these authors. Organisms do not transfer only genes to their descendants. All changes promoted in the environment by a niche constructor form a true legacy that remains for the subsequent generations and other organisms, even after the constructor's death. This legacy can change ecological pressures, creating a special evolutionary niche. Unlike genetic inheritance, ecological inheritance is not related to the niche constructor's reproductive capacity. This implies that the constructor's legacy is not necessarily transmitted only to other related individuals, and this legacy may affect any populations that are mediated by some biotic or abiotic component. Likewise, the legacy's transmission is independent from replicating mechanisms and requires only intergenerational persistence for maintaining

any changes that result in selective pressures (Odling-Smee et al., 2003).

Nevertheless, unlike the other species, humans change their surrounding guided mainly by cultural processes (see Albuquerque and Ferreira Júnior, 2017). That is, the alterations that we perform on the environment are based in our learning and/or in socially transmitted information (Ellis, 2015; Laland and O'Brien, 2012).

The domestication of species (including the emergence of the agriculture and the livestock raising) is, perhaps, the human activity that is most representative of the cascading effects caused by the change in selective pressures in the environment. Through domestication, we have fixed morphological and behavioral phenotypes that would be deleterious without human management (such as indehiscent fruits in cereals and pulses, reduction in size and shape of horns in caprines, no longer needed for mate competition, and reduced reactivity to humans in domesticated animals) (Zeder, 2016). These activities also have unprecedented impacts on the distribution of useful species around the world, as well as on the emergence of new species and subspecies (Boivin et al., 2016). Moreover, the agriculture emergence had a great feedback to human cultural evolution because it may have facilitated the evolution of cooperative behavior, and other changes in cultures, resulting in explosive human population growth (Zeder, 2016).

Another example of niche construction from the use of soil for agricultural management is found in the Amazon regions known as “black earths” (Arroyo-Kalin, 2010). Archeological records demonstrate that these areas have been used since the late Pleistocene as human settlements and are the sites of development for a number of rudimentary agricultural techniques (Heckenberger et al., 2007). The use of these areas for slash and burn agriculture over centuries by pre-Columbian populations formed the current highly fertile anthropogenic soils (Quintero-Vallejo et al., 2015). Land management in these localities substantially changed the soil conditions, generating a completely distinct evolutionary niche that remains to the present day conditioned by the composition of the soil bacteria community (Barbosa Lima et al., 2015) and the distribution patterns of the plant species (Quintero-Vallejo et al., 2015). The ecological inheritance that accompanies the Amazonian black earths has conditioned, additionally, the land-use patterns of current populations, as has been shown by comparative research on agricultural practices in Amazon regions (Fraser et al., 2011a; Junqueira et al., 2016). Cropping in agroforest plots developed on these anthropogenic soils differ in floristic structure, diversity, and composition, and the soil in these areas usually produces greater plant species richness and number of individuals when compared to other soil types (Fraser et al., 2011b).

One of the best documented cases of a human-created niche affecting its own species is the case of lactose tolerance development in adults (Albuquerque et al., 2015; Gerbault et al., 2011). Milk is the main energy source for most mammal species in the young stage. With maturity, there is a decline in the production of the enzyme responsible for milk digestion, which makes the maintenance of milk as a food resource impossible. With the advent of animal domestication strategies, the adoption of a pastoral culture, and the development of milk-producing techniques, a new evolutionary niche was created. Because it is an extremely rich source of protein and fat, milk may have represented an energy alternative in the periods between harvests or in periods when few grains were available (Holden and Mace, 2014). Adult individuals who were able to digest lactose therefore had an advantage in calorie consumption, and the trait for lactose tolerance was then fixed in these populations (Holden and Mace, 2014).

The study of the interaction of organisms from the NCT perspective has demonstrated the importance of niche constructors as key elements in the structure and functioning of ecosystems. Humans have been considered a “hyperkeystone” species due to

the transformations and impacts they have on nature's interaction webs (Worm and Paine, 2016). The role of the human species as one of the most important niche constructors is unquestionable. The use of this theoretical benchmark to analyze the interactions between humans and the environment may represent a promising intellectual strategy for understanding the current scenario and for predicting more realistic future ecosystem conditions. Nevertheless, all efforts may fail if we do not consider that, by altering the environment, future generations will inherit not only environments (ecological inheritance) but also social information.

Case study: effect of cattle grazing at a landscape scale

For many years, our research group has monitored social-ecological relations in an environmental conservation area in the Northeast of Brazil. Our study site is the Araripe National Forest (*Floresta Nacional do Araripe* – FLONA-Araripe), a conservation unit established with the goal of reconciling nature conservation with the sustainable use of natural resources. The case study that follows strongly considers the interactions between humans and the environment from an ecological and evolutionary perspective. Our dataset provides evidence for the need of greater integration between ecology and humans to understand the range of human activities in the environment.

FLONA-Araripe encompasses an area of approximately 39,000 ha, consisting of a mosaic phytophysiognomies including *cerrado* (*sensu stricto*), *cerradão*, *carrasco* (similar to a xerophytic vegetation), and semideciduous seasonal forests (Ribeiro-Silva et al., 2012). Inside FLONA-Araripe, human populations subsist, mainly of the extractivism of plants such as *Dimorphandra gardneriana* Tul. (commonly known as fava d'anta), *Caryocar coriaceum* Wittm. (commonly known as pequi) and *Himatanthus drasticus* (Mart.) Plumel (commonly known as janaguba) (Baldauf and Santos, 2013; Feitosa et al., 2014; Sousa Júnior et al., 2013).

Prior to the establishment of this conservation unit, human groups lived inside the area, managing these resources, and using its space for agriculture and cattle ranching. With the establishment of this unit in 1946, people were forced to leave the region, settling in adjacent areas. Since 2004, with the creation of the FLONA-Araripe management plan, cattle ranching has been completely prohibited in the unit, and fencing was erected in some areas to avoid animal access (Ibama, 2004). However, this activity had already been declining for a longer time. Cattle ranching in forested areas, especially in conservation units, are common worldwide. In some units, this activity is encouraged because potential benefits are associated with grazing such as exotic and invasive plant control and the increase of dispersal services for plants with large diaspores (Borman, 2005; Bradford et al., 2002).

We employed different techniques (such as collective subject discourse analysis, community mapping and scoring exercises) to access the perceptions of local people regarding the effect of these actions (Flona establishment) on their practices and the natural resources in the region. One key observation is that the prohibition of cattle ranching in the region affected local ecological relations, particularly the ones centered on a species that provides edible fruits, the pequi (*Caryocar coriaceum*). Locals stated, for example, that the presence of cattle in the forest increased the number of trails, which favor pequi populations; pequis are heliophytes and prefer open areas for development. Additionally, according to oral history and ethnobiological evidence, cattle ate *C. coriaceum* fruits and, consequently, influenced the dispersal of this specie in the region (Silva, 2014).

According to people's perception, the vegetation at FLONA-Araripe has increased due to the removal of cattle from the forest (Silva, 2014). This increase in vegetation has negatively affected

the abundance of many useful heliophytic species, such as *C. coriaceum*. Evidence from aerial images taken over time shows an increase in the density of the local vegetation. According to the perceptions of local residents, this increase is the result of the prohibition of cattle ranching in the region, which has also increased the richness of species of little or no significance to local communities. Because the region comprises a mosaic of different vegetation types, the *cerrado* (savanna) is showing signs of conversion into a denser formation. This evidence, combined with human ecology data, indicates that local populations have mapped the entire region into approximately 304 cultural landscapes that are essentially named according to utilitarian attributes and the presence of locally important resources (see Silva, 2014; Silva et al., 2017).

Because cattle ranching had served as the base of the local economy, after its prohibition, people had to adjust their survival strategies to fit an economy focused on extractivism of plant products. Currently, pequi fruit is the main product and the central element of the economy of the entire region (Sousa Júnior et al., 2013). Therefore, the argument is that cattle ranching, which was previously the foundation of the local economy, favored the heliophytic plant populations, but after the prohibition of this practice, the economy shifted toward plant populations of economic interest.

This new pequi-extraction-centered economy affected both the species and the sociocultural systems. People started to develop different levels of attention to the species (Sousa Júnior et al., 2013) such as fruit harvesting in native populations and fruit harvesting in specially nurtured (not cultivated, but with the competitor species eliminated, for example) populations. The care provided by local populations with the intention of stimulating fruit production in the pequi have led to a phenotypical divergence of this plant in the region, with an increase in its morphological diversity (Sousa Júnior et al., 2016). However, we still do not know if such diversity has a genetic basis. With the increase in local extraction, one of the most important practices in the region is oil production from fruits (a visual ethnography of this practice is found in Cavalcanti et al., 2015a). At harvest time, many extractivists camp in the forests to produce oil, and they collect wood from the forest to cook the fruit. At least 28 species of woody plants are used as fuels to produce pequi oil (Cavalcanti et al., 2015b), with collection pressure being higher on 50% of these species. This finding demonstrates the impact of using a non-timber forest product on other woody species.

If we used the perspective of chronic anthropogenic disturbances to interpret the transformations in the FLONA landscape, we would probably argue that cattle grazing exerted a continuous and low intensity disturbance on the local ecosystem, both by the consumption of certain plant species (including the pequi fruit), as by trampling, which caused abiotic changes (including the formation of clearings, which certainly modified the local microclimatic conditions). After the ban on livestock in the region, local vegetation would be reestablishing the conditions prior to the disturbance (supposedly human-free and "natural" conditions), evidencing the resilience of the local tree community. However, not all aspects of ecosystem functioning have been restored to previous conditions. In this case, there would be three possible explanations: (1) cattle grazing resulted in irreparable changes in the studied ecosystem, which would confirm the idea of chronic anthropogenic disturbances (see Singh, 1998); (2) there has not yet been sufficient time for the ecosystem to re-establish itself to the conditions prior to the disturbances; or (3) new chronic anthropogenic disturbances prevent the restoration of the studied ecosystem to "natural" conditions resulting in "new" environments.

In our perspective, there are some flaws in this viewpoint. At first, there are operational and practical matters. Using proxy variables to estimate chronic anthropogenic disturbances at the Flona

would be misleading because it disregards the historical changes on the human-ecosystems interactions. Likely, the population density around the Flona, and the distance from the Flona to human settlements, urban areas and highways have not changed so much, but the human activities on this ecosystem changed greatly. Therefore, researchers would need to resort to some historical methodology to record the preterit livestock density, because the current proxy variables could not explain the human alteration on this landscape. Therefore, the changes on the use of forest resources in the Flona along time exemplify the flaws on this proxy variables, because these measures have not changed.

There are some heuristic flaws in this approach too. At first, the viewpoint that the establishment of conservation areas may induce the forest ecosystems to return to a “natural” and pristine stage makes no sense. Although the Flona vegetation is becoming denser, it cannot be restored to the same conditions observed before the human occupation. Human prehistoric populations certainly have changed the structure and composition of the Cerrado ecosystems, and influenced the selective pressures on species for thousands of years (Bueno et al., 2013; Galetti, 2004; Piperno et al., 2017; Villagran et al., 2017). We believe this kind of preservationist discourse from scientific academy may influence the discourses and the attitudes of the environmental managers who typically tend to adopt management strategies which usually requires removal of local residents and their land management practices (see Law and McSweeney, 2013). Furthermore, the chronic anthropogenic disturbance approach lacks an evolution base. In this case study, we argue the extractivism just not causes disturbances, but also acts as an additional selective pressure on species, directly, by changing phenotypic characteristics on target species, or indirectly, through cascade effects on ecosystems.

Conversely, from the perspective of niche construction, we propose that the scenario shows that human action modified biotic and abiotic factors in the ecosystem with the intention of increasing the productivity of the herds (through selection of areas for grazing, intentional clearing to facilitate the movement of herds, and the collection of forage plants). The cattle was also involved in niche construction processes, both by the selective behavior of plant species consumption and by the abiotic modifications resulting from the consumption of plant biomass and trampling (promoting the emergence and increase of clearings). These co-constructed niches resulted in cascade effects on the targeted species of cattle grazing (especially pequi) and on organisms not directly involved in this interaction, including mainly animals that consume the fruits of pequi and tree species that compete with pequi. Subsequently to the ban on livestock farming in the region, the entire ecological community responded to habitat changes that were bequeathed by cattle grazing, as a type of ecological inheritance. In this sense, most of the tree flora responded to changes (“closing” the clearings, and consequently, reducing the probability of occurrence of fires) forming shady habitats that make it difficult for the seedlings of heliophytes species to settle. Animals that consume the pequi began to act as their main dispersers (in substitution to the cattle herd), altering the pequi populations. Finally, people responded to the ban on livestock through cultural changes, adopting vegetal extractivism as the main source of subsistence, engaging in new activities with the potential to greatly modify the local ecosystem.

The new local subsistence economy, centered mainly on pequi extractivism, results in new patterns of use of plant resources, including wood collection for firewood and pequi oil production. These activities may affect the composition and structure of woody plants populations (in ways that are not easily predictable because these species are sometimes favored and other times more intensively collected due to variations in other local practices). Additionally, cooking the pequi fruit for oil production may affect the population growth rate of the species by

decreasing the number of viable propagules in the soil banks of the forest.

Moreover, in the past, cattle grazing favored other ecological relations in the forest, such as the one between dung beetles (Coleoptera: Scarabaeidae) and the pequi tree. At FLONA-Araripe, pequi diaspores are buried by these beetles under the canopies of the parent trees (Santos et al., 2016). This finding led us to hypothesize that the cattle's grazing favored pequi dispersal by making available a large amount of fecal matter, which contained pequi fruits that could be buried by the beetle in different forest patches. Consequently, with the presence of cattle, the dung beetle provided an ecological service by compensating for the absence of frugivorous dispersers of large seeds. By burying the diaspores, these beetles assist in protecting the seeds, freeing them from predator action (Nichols et al., 2008). Presently, burying the fruits under the tree canopies helps increase the aggregated distribution pattern, which can increase in the mortality rate due to competition, predation, or pathogen attack; however, from a conservationist perspective, this effect results in substantial loss of genetic diversity (Jordano et al., 2006). To avoid this loss, the coexistence of these beetles with frugivorous, large-sized animals, such as cattle, would be essential to enable long-distance dispersal events. Thus, by burying the pequi fruits contained in the feces of these exotic animals, the beetles free them from pathogenic agents and improve the environment for germination by promoting soil aeration and fertilization (Andresen and Levey, 2004; Lawson et al., 2012; Vander Wall and Longland, 2004). In a small-scale experiment to estimate the role of the beetle in the abundance and richness of species, we used traps containing either cattle feces only, fruits only, or a combination of feces and fruit. Greater species richness and abundance were found (total of 511 individuals of 22 species) in traps combining feces and fruit compared to traps where these baits were offered separately (Santos, 2016).

Oral accounts on the role of cattle as pequi fruit dispersers have ecological support. Many mammal species from the past, such as wild horses, giant armadillos, mammoths, and giant sloths certainly included fruit in their diets, acting as important dispersers for many plant species, particularly for the species with large fruits (Janzen and Martin, 1982). However, at the end of the Pleistocene, many mammals, especially those heavier than 44 kg, were extinct in many regions around the world. In South America alone, approximately 50 genera were extinct, corresponding to more than 80% of the mammals heavier than 44 kg (Koch and Barnosky, 2006). Thus, the extinction of these mammals may have changed the distribution, demography, and genetics of many plant populations (Janzen and Martin, 1982).

Serving as replacements of extinct megafauna, non-native domesticated animals such as cattle and horses consume fruits and disperse seeds for many plant species that have large fruits without local native dispersers (Janzen and Martin, 1982). The presence of these exotic species has contributed to the dispersal of several plants, especially those with large fruits and seeds (Donatti et al., 2007). Therefore, these exotic animals, introduced in the colonial period, could be important large seed dispersers and invasive weed controllers when in controlled densities (Galetti, 2004).

Due to the absence of large dispersers, plant species with large fruits and seeds are dispersed to short distances from their sources by predatory hoarding rodents such as the agouti (*Dasyprocta* spp.), contributing to an aggregated distribution pattern in these plant species (Donatti et al., 2007; Guimarães et al., 2008; Jansen et al., 2012). This can influence the genetic flow and intrapopulation genetic structure of these plant species (Jordano et al., 2006; Nathan and Muller-Landau, 2000). In the absence of frugivores, many plant species are destined to local extinction due to the loss of dispersers (Wright, 2003). The pequi is presently subjected to intense extraction, and populations are composed of a small number of young

individuals (Almeida, 2014), with indications that mammalochory is absent (Santos et al., 2016). The lack of mammalian dispersers probably results from the combined hunting of vertebrates in the region (Silva Neto et al., 2016), whether to meet calorie demands or for local medicinal practices.

Although we have essentially addressed the effects of human actions based on a framework of ecological implications, what is shaped is a social-ecological system. The pequi in the previously discussed scenario, more than other plants in the region, occupies a central sociocultural role because it structures lifestyles, beliefs, habits, and economic relations. Many local incomes depend on the extraction of fruits, operating within a noncooperation framework of extractivist groups who seek to maximize profits (Silva et al., 2015). If this activity is not regulated with the participation of the different social actors, this scenario may lead to a tragedy of the commons. The tragedy of the commons can be described as follows: when people use collective resources, they automatically decrease common benefits because collective resources tend to be used excessively (to the point of exhaustion) if there are no charges and/or regulations, leading to a predictable scarcity of common resources (Hardin, 1968).

Local regulatory actions have been discussed for the extraction of some species in the region, including for *H. drasticus* (Mart.) Plumel. The latex from this species, when mixed with water, is known as “janaguba milk,” popularly used as a treatment for conditions such as gastritis, anemia, inflammation, worms, and some forms of cancer. Evidence reported in the literature suggests that the extraction of *H. drasticus* bark for obtaining latex increases this species’ reproductive phenology (Baldauf et al., 2014a). Additionally, Baldauf and Santos (2014b) demonstrated that this species is resistant to extraction, despite its slow regeneration, particularly in denser forested areas.

The entire region, including the area surrounding FLONA-Araripe, has been and still is a site of intense human activity. The region has an extensive area of monodominant *Attalea speciosa* Mart. Spreng forest (Arecaceae – popularly known as babassu), the abundance and geographic range of which has been favored by human activities. This resulted in an economic and cultural niche focused on the exploitation of this species, which has become the foundation for the family economy of many extractivist communities, especially of women, who call themselves “babassu coconut breakers”¹ (Almeida et al., 2016; Campos et al., 2015). Historical (documents) and social-ecological (oral accounts and perception) evidence indicates that the activities that favored this species began even before the European settlers arrived in the region and were strengthened by forest clearing for sugarcane cropping. The local landscape has coincidentally evolved, as the human actions affecting the landscape were not intended to favor this species.

The case study presented allows for some considerations. If we used the ecological approach of chronic anthropogenic disturbances, the first difficulty would be to access past human actions, since most researchers associate present proxies’ variables of human action with the current ecological variables. Furthermore, even if we tried to estimate past proxies’ variables (for example, cattle density in past decades) it would be difficult to predict the observable net effects derived from different interactions between humans and the biota because this approach lacks an evolutionary perspective. However, the main problem may be the interpretation of this local scenario. Instead of considering humans as the cause of disturbances that impede the ecosystem from reaching its climax stage, we propose that we are modifying our ecological niche all

the time, in a manner that strongly influences the evolutionary trajectory of other species, and consequently, our own evolutionary trajectory.

Concluding remarks

Regardless of the approach adopted by scientists, humans have shaped and will continue to shape global biodiversity through long- and short-term activities. The recognition of this contribution is essential for the contemporary understanding of the interactions that exist between our species and ecosystems in order to predict future transformations (Boivin et al., 2016). The development of a research program (*sensu* Lakatos, 1980), in which the human being is effectively considered in ecological experimentation is urgent. The challenge faced by ecologists, who have been invited to this way of thinking for at least 20 years, is to study our species’ behavior as well as the entire extent of our activities.

The NCT concept, by its inherent comprehensiveness, could easily accommodate chronic disturbance-centered approaches. However, an accommodation that does not result in theoretical, epistemological, and methodological conflict requires that the concept of “negative effects” that emerges subjacent to the chronic disturbances concept be abandoned. Furthermore, this concept should be rejected by ecologists and replaced by the idea of regarding humans as constructors of new niches, an idea that incorporates the dynamic character of interaction webs. Adopting this perspective would allow us to reevaluate our interactions with nature and promote an understanding of the forces that shape our behavior and cognition, so that we can do what we do best as a species: construct niches. No evidence exists to support the idea of pristine or untouchable environments since our species appeared and dispersed on the planet. From that moment until this day, humans have had the entire Earth as their “natural habitat.” This idea does not imply that concerns about the conservation of other species should be reduced but rather suggests the necessity of thinking about conservation and adequately managing the resources used (biological or not) in a more dynamic and realistic context.

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¹ Our team has produced a documentary about the human activities concerning this species, and this documentary can be found at the following link: <https://www.youtube.com/watch?v=pAyZ52FAvos>.

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