EVOLUTIONARY BIOLOGY

Orangutans venture out of the rainforest and into the Anthropocene

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Conservation benefits from understanding how adaptability and threat interact to determine a taxon's vulnerability. Recognizing how interactions with humans have shaped taxa such as the critically endangered orangutan (*Pongo* spp.) offers insights into this relationship. Orangutans are viewed as icons of wild nature, and most efforts to prevent their extinction have focused on protecting minimally disturbed habitat, with limited success. We synthesize fossil, archeological, genetic, and behavioral evidence to demonstrate that at least 70,000 years of human influence have shaped orangutan distribution, abundance, and ecology and will likely continue to do so in the future. Our findings indicate that orangutans are vulnerable to hunting but appear flexible in response to some other human activities. This highlights the need for a multifaceted, landscape-level approach to orangutan conservation that leverages sound policy and cooperation among government, private sector, and community stakeholders to prevent hunting, mitigate human-orangutan conflict, and preserve and reconnect remaining natural forests. Broad cooperation can be encouraged through incentives and strategies that focus on the common interests and concerns of different stakeholders. Orangutans provide an illustrative example of how acknowledging the long and pervasive influence of humans can improve strategies to preserve biodiversity in the Anthropocene.

INTRODUCTION

Humans have been described as the world's greatest evolutionary force (*1*). A long history of human hunting, habitat modification, translocation, and domestication has shaped the distribution, abundance, morphology, and behavior of most modern taxa (*2, 3*). Widespread Pleistocene extinctions and the current extinction crisis also demonstrate that human activities threaten many species (*4, 5*). These human impacts have increased since at least the late Pleistocene (*2*), and this trend will likely continue as we advance into the Anthropocene, a new epoch proposed to acknowledge the pervasive worldwide impact of human activities (*6*). Our limited understanding of how adaptability and threat interact to determine species' vulnerability to extinction hinders our ability to anticipate the implications of these trends for conservation (*7*). Investigating how humans have shaped the abundance, distribution, and behavior of species in the past may help inform conservation planning and practice for a future increasingly dominated by human activities (*2–4, 7, 8*).

Orangutans provide a valuable opportunity to explore the potential of this approach. Since the 1970s, the charismatic, critically endangered orangutan has been an icon of wild nature under threat due to current human activities (*9, 10*). However, orangutans have been subject to human influence for at least 70,000 years (*11, 12*). Recent research has also documented the orangutan's flexibility in response to human alteration of their habitat, with some populations living in previously logged forest (*13, 14*) and even persisting in human-dominated environments such as forestry and palm oil plantations and agroforestry landscapes, engaging in behaviors including feeding on crops and building nests in exotic trees, including oil palms (Fig. 1) (*15–18*). Despite these observations, orangutans retain their status as symbols of fragile, untouched nature (*9, 10*), and recent findings on adaptive behavior have not yet been broadly incorporated into orangutan conservation strategy (*19*). This is not surprising because conservation practice lags behind research (*20, 21*), but it does hinder effective conservation action on behalf of orangutans.

A clear understanding of how orangutans have responded to prolonged exposure to humans can offer new insights into their vulnerability and resilience to modern threats. Although climate-driven vegetation change has been commonly cited as the cause of the marked decline in orangutan distribution and abundance after the late Pleistocene [126 to 12 thousand years (ka) ago] (*22–26*), some researchers have suggested that human hunting contributed significantly to this decline (*24–27*). A comprehensive assessment of these competing hypotheses has yet to be made. Here, we review the available paleontological, archeological, and genetic evidence to assess the relative impacts of environmental factors (specifically, climate-driven vegetation shifts) and human impacts (specifically, human hunting and habitat alteration) on orangutan populations in the past. We then discuss how our conclusions can enhance current interpretations of orangutan behavior and inform orangutan conservation strategy in an increasingly human-dominated world.

HOW DID HUMANS INFLUENCE ORANGUTANS IN THE PAST?
Setting the stage

A review of orangutan natural history is necessary for examining the pressures, environmental or human-induced, that led to their decline after the late Pleistocene. Populations of wild orangutans persist on the Southeast Asian islands of Borneo (*P. pygmaeus*) and Sumatra (*P. abelii*

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Fig. 1. Orangutans in human-dominated landscapes. Although it was long assumed that orangutans were not capable of coexisting with intensive human activity, they have recently been found living in anthropogenic landscapes that are heavily altered by humans in Borneo and Sumatra. Here, we show examples from (**A**) a forestry plantation in East Kalimantan, Indonesia (photo credit: Stephanie N. Spehar), (**B**) an oil palm plantation in Sabah, Malaysia (photo credit: Marc Ancrenaz), and (**C**) regenerating forest near a former mining concession in Central Kalimantan, Indonesia (photo credit: Tine Geurts).

and the newly described *P. tapanuliensis*) (*28*). All species of orangutan are considered critically endangered due to human activities, and their population trends are listed as decreasing (*29*). Orangutans are the largest primarily arboreal mammals and have few large predators other than humans (*30*). Their preferred diet consists of ripe fruit, but they exploit many other foods, notably lower-quality "fallback" foods, when fruit is scarce (*31*, *32*). Orangutans generally live at low densities (1 to 3 individuals/km^2) and are unique among apes in being semi-social, with adult individuals spending much of their time alone (*33*). However, these generalizations do not capture the variation in diet, locomotor patterns, social and reproductive behavior, and culture (for example, tool use, vocalizations, nest building, and other behaviors) documented among orangutan populations (*30*). This variation appears correlated with local ecological conditions, with populations in more fruit-abundant habitats exhibiting higher densities, lower dietary breadth, more frequent sociality, and more complex cultural repertoires than those in fruit-poor habitats (*30*). Some of this variation may be based on genetic adaptations [for example, the more robust jaws found in the northeastern Bornean orangutan (*P. pygmaeus morio*) may facilitate their wide dietary breadth by allowing them to exploit tough foods other orangutans generally avoid (*30*)]. However, in many cases, it appears to reflect orangutans' considerable behavioral flexibility, a feature that represents a broad adaptation by this long-lived, highly mobile animal to spatial and temporal change in local environments (*34*). This flexibility not only can increase adaptability to environmental change but also confers a clear limit, as traits that support flexibility (for example, large brains and associated long juvenile periods that facilitate development and learning) may also inhibit species' ability to respond to rapid changes

and acute threats: Long generation lengths mean that genetic adaptation happens very slowly and that populations cannot recover quickly from losses due to hunting, capture, or disease (*34*).

The Miocene ancestors of orangutans lived in South or East Asia, with the genus *Pongo* originating at the Miocene/Pliocene boundary 6 to 5 million years (Ma) ago and reaching the southernmost extent of their historical range in Southeast Asia by 2 to 4 Ma ago (*24*). The late Miocene (12 to 5 Ma ago) saw the onset of the Asian monsoon system (*35*) and the initiation of El Niño Southern Oscillation events (*36*) that led to the irregular mast fruiting cycles characteristic of Southeast Asian forests (*37*). The Pleistocene (2.6 Ma to 12 ka ago) also saw marked climatic shifts in the form of cycling glacial and interglacial periods. During the extended glacial periods, the climate was generally cooler, drier, and more seasonal than in the briefer interglacials. Glacial climates resulted in reduced forest cover, leading to fragmentation and greater temporal and spatial heterogeneity in food availability (*24*). The resulting intermittent food stress and competition may have favored the highly dispersed sociality characteristic of modern orangutans (*38*).

During the Pleistocene, multiple *Pongo* species occurred across southern China, mainland Southeast Asia, and the Sunda Shelf, the landmass connecting the present-day islands of Sumatra, Java, and Borneo. Fossils indicate that the distribution of orangutans contracted toward the end of the late Pleistocene (126 to 12 ka ago) and that, by the Pleistocene/Holocene boundary (12 ka ago), *Pongo* remained only on Borneo and Sumatra (Fig. 2 and table S1) (*22–26*), which represents about 20% of their original range. In addition to this reduction in distribution, a comparison of the ratio of orangutans to other primates (cercopithecoids and hylobatids) between fossil and modern sites suggests that the density of orangutan individuals also declined after the late Pleistocene (Table 1 and table S2). The fact that the ratios of orangutans to other primates is significantly lower today than in the Pleistocene indicates that orangutan densities have declined significantly since the Pleistocene, while the densities of other primates have not changed as substantially. A greater accumulation of orangutan remains versus other primate remains at Pleistocene sites could be the result of preferential hunting by humans. However, given that human hunting caused the accumulation of only one set of fossil remains analyzed here (Niah Cave in northern Borneo, used by humans from 50 to 4 ka ago) (*39*, *40*), we do not think that this significantly influenced our assessment of the differences between relative primate densities in the past and the present, nor do we consider taphonomic factors, such as preferential bone accumulation by porcupines or similar species, as offering plausible explanations for these trends. These mechanism cannot account for why the relative densities of orangutans have decreased substantially from the Pleistocene to the present, while densities of other primates do not show comparable declines. Finally, genetic evidence also indicates that orangutan populations have declined since the late Pleistocene. Specifically, these data suggest that Sumatran populations were much reduced from around 24 ka ago, and Bornean populations were reduced between 2000 and 200 years ago (*27*, *41*, *42*).

Explaining the Pleistocene orangutan decline
Two main hypotheses have been proposed for the decline in orangutan distribution and abundance after the late Pleistocene: environmental impacts and human impacts. The environmental impact hypothesis postulates that the orangutan decline resulted from climate-driven vegetation change. According to this hypothesis, increased climatic fluctuations beginning in the early Pleistocene (2.6 Ma to 780 ka ago)
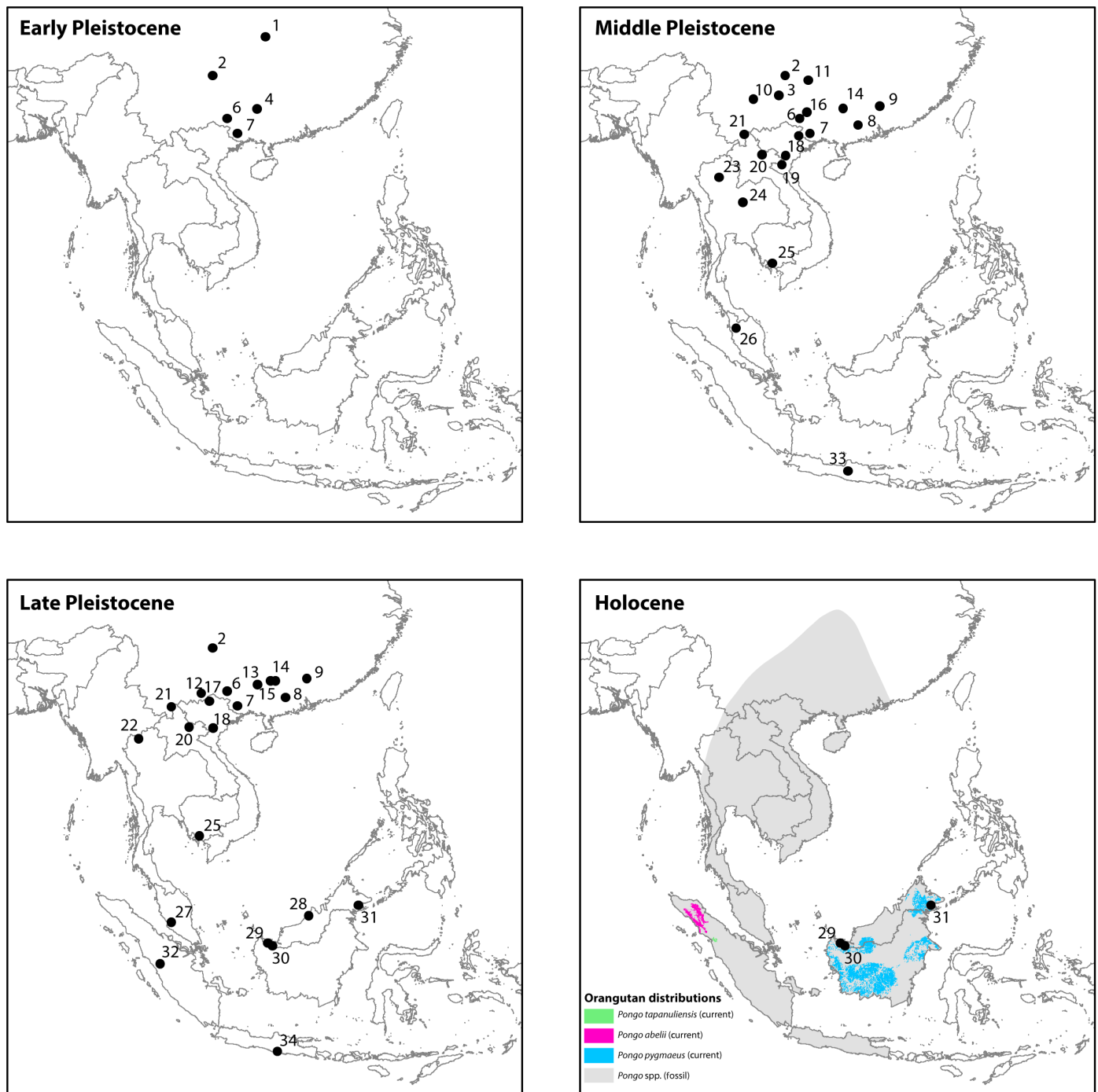
Fig. 2. Orangutan distribution from the early Pleistocene to the present. The past distribution is based on fossil sites (black dots); the current (as of 2015) and entire past orangutan distribution is indicated on the Holocene panel. Location of study sites and references are provided in table S1.

resulted in a gradual southward shift of tropical and subtropical zones in East Asia, increasing seasonality, fragmenting habitat, and possibly constricting orangutan populations, making them more vulnerable to extinction (*22*). Then, during the Last Glacial Maximum (LGM) (24 to 18 ka ago), the climate became significantly cooler and drier. According to most modeling and paleoecological analyses, this significantly reduced the extent of closed-canopy tropical forest in Southeast Asia,

and large areas were replaced with more open, savanna-like habitat (*23*, *43*, *44*). Refugia remained in the vicinity of modern-day Borneo and Sumatra, and evidence suggests the presence of a north-south nonforest corridor bisecting the Sunda Shelf and preventing movement of orangutans and other forest animals between the two areas (*43*). In the forests that remained, the climatic conditions became more seasonal (*22*–*24*, *44*). According to the environmental impact

Table 1. Ratio of *Pongo* to cercopithecoids and hylobatids at fossil sites (using number of individual craniodental specimens) and modern sites (using densities of individuals per square kilometers). Complete data set and sources are provided in table S2.

	Fossil sites (*n* = 14)* (number of fossils)	Modern sites (*n* = 13) (individuals/km²)
Mean across sites		
Pongo	182 ± 80.59	1.81 ± 0.32
Cercopithecoid†	218 ± 28.19	47.94 ± 11.02
Hylobatid	6 ± 2.83	8.75 ± 1.22
Ratios		
Pongo: Cercopithecoid	0.84 ± 5.23	0.04 ± 0.03
Pongo: Hylobatid	30.33 ± 27.05	0.21 ± 0.06

*Only those fossil localities with *n* > 20 *Pongo* specimens were included to minimize sampling biases.   †Only presented for those sites for which counts or density estimates of both *Presbytis* and *Macaca* were available.

Fig. 3. Canopy cover at fossil and modern orangutan sites across Southeast Asia. Sites are arranged from oldest (bottom) to youngest (top). Ecological conditions for fossil sites are inferred using a synecological method that uses the relationship between faunal communities and the relative proportion of continuous canopy cover at a site (*100*). Faunal and age references are provided in table S3.

hypothesis, orangutans became extinct throughout much of their range by the end of the late Pleistocene because of either the disappearance of suitable habitat or the isolation of populations into small fragments, and only Borneo and Sumatra retained sufficiently large and productive rainforest areas to permit the persistence of viable populations. When closed-canopy forests expanded again near the beginning of the Holocene, sea levels had risen, and orangutans were unable to re-expand into parts of their range in which they had become regionally extinct (for example, Peninsular Malaysia) (*22, 23, 25, 26*). The fact that other fruit-eating, forest-dwelling Asian primates (for example, gibbons and macaques) did not suffer similar population restrictions throughout the Pleistocene is explained by the orangutan's unique combination of features—a preference for fruit and higher absolute energetic requirements due to larger body and brain size—which made them less able to withstand extreme seasonality than gibbons or macaques (*22*).

The environmental impact hypothesis gains some support from fossil evidence. At several orangutan fossil sites (for example, Batu Caves in Malaysia and Punung in Java), paleoecological analyses indicate a shift to more open, savanna-like vegetation in the late Pleistocene, followed by the absence of orangutans in the fossil assemblage (*26, 45*). However, there are several lines of evidence that challenge the environmental impact hypothesis. First, it appears that in general, *Pongo* adapted and thrived throughout previous Pleistocene glacial-interglacial cycles, despite the fact that the environmental impacts were similar to those of the LGM (*23*). Some researchers have suggested that a contraction of the orangutan range began earlier in the Pleistocene, but this does not appear to be borne out by the fossil evidence (table S2) and the most frequently cited source (*22*) finds that *Pongo* was widely distributed across Southeast Asia and southern China throughout the Pleistocene. Second, an analysis of the ecological conditions at orangutan fossil sites actually shows that orangutans inhabited both forested and more open semi-forested environments throughout the Pleistocene (Fig. 3). For example, palynological (fossil pollen) analysis from Niah Cave, Borneo indicates that shifts between lowland rainforest and more open vegetation types occurred there numerous times over the past 50,000 years; orangutans are found in the fossil assemblage at Niah throughout these shifts, albeit at varying frequen-
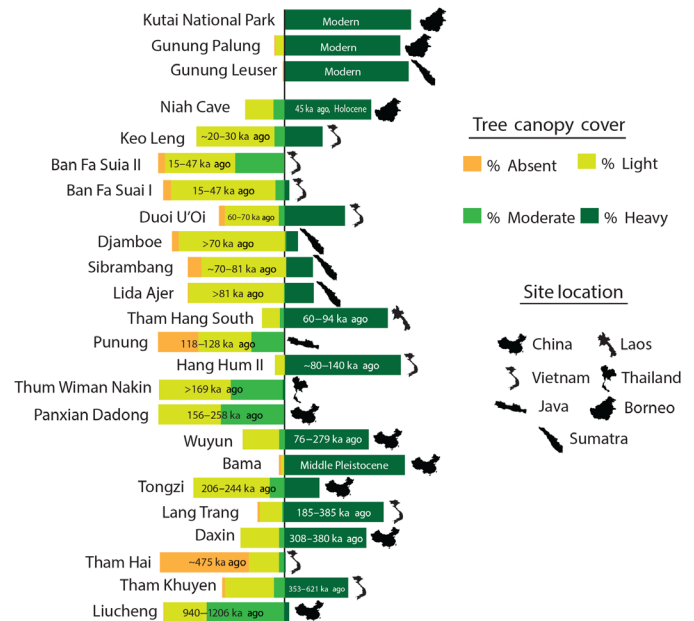
cies, and only disappear during the Holocene (*39, 40, 46*). This suggests considerable ecological flexibility on the part of orangutans, which is reinforced by behavioral data from modern orangutan populations (*30*). Studies of modern orangutans indicate that they exhibit considerable dietary plasticity, facilitated by features of their morphology and physiology that were presumably selected for by long periods of extreme food stress (*31, 32*). The dietary breadth of orangutans is often greater than that of sympatric gibbons (*32*), casting doubt on the assumption that ecological constraints are the sole explanation for why the distribution of orangutans was significantly reduced during the late Pleistocene, while the distribution of other primates (for example, gibbons) was not (*22*).

On the other hand, the human impact hypothesis postulates that humans were a principal cause of the decline of orangutan populations that began near the end of the late Pleistocene. The major contribution of human activities, especially hunting, to the range reductions or extinctions of many large animals in the late Pleistocene and Holocene is well established (*2, 4*). Orangutans, being relatively conspicuous and slow-moving, appear to be easier targets for hunters than many other forest-dwelling mammals. Remains at Niah Cave in northern Borneo, around which orangutans have been absent since at least the earliest historical times, show that orangutans were commonly hunted from the terminal Pleistocene and possibly as early as 45 ka ago (*39, 40, 47*). Orangutans have also been hunted throughout their known range in modern times (*48–50*). This hunting does not have to be intensive to have an appreciable impact, as the orangutan's low rate of reproduction means that even a minor increase in the morality can contribute to range contraction and density reductions, with simulations suggesting that annual offtake rates of only 2 to 3% are unsustainable regardless of population size (*51*). Finally, the abrupt and marked decline in orangutan distribution around the Pleistocene/Holocene boundary mirrors patterns seen in other human-driven extinctions in the prehistoric and historic

record (for example, the elimination of the moas in New Zealand and giant lemurs in Madagascar within a thousand years of first human contact) (*2*, *4*).

What role did humans play?

Evaluating the human impact hypothesis requires examining the correspondence between the fossil and genetic evidence for orangutan range restrictions on the one hand and between the archeological and fossil evidence for human hunting and environmental impacts on the other. Many date estimates have wide confidence intervals, and the archeological and fossil record in many parts of Southeast Asia is sparse, which means that this correspondence is not precise. However, demonstrating a general relationship between human impacts and orangutan population declines across the region, especially given the absence of strong links between environmental impacts and orangutan declines, would suggest that the human impact hypothesis can be supported.

Earlier hominins, notably *Homo erectus*, were present in Southeast Asia from at least 1.5 Ma ago (*52*), but current evidence suggests that they did not regularly hunt large animals, at least not with the efficiency required to cause local extinctions (*53*). Modern humans (*H. sapiens*) arrived on the Southeast Asian mainland at least 70 ka ago and possibly earlier (*11*, *12*). They quickly moved into more accessible areas of island South-East Asia, with the archeological record indicating that they were present in western Sumatra between 73 and 63 ka ago, had colonized the northern coast of Borneo 50 ka ago, and were in Java at least 40 ka ago (*11*, *12*, *39*, *54*). Significant human dispersal into the modern-day orangutan strongholds, the forested interiors of Borneo and Sumatra, probably did not occur until the Pleistocene/Holocene boundary (12 ka ago) and much later in many cases (*55*, *56*), although the presence of modern humans in the Padang Highlands in western Sumatra at least 63 ka ago indicates that they were capable of dispersing beyond coastal areas (*12*). Current evidence indicates that early inhabitants of Southeast Asia used a subsistence strategy that combined wild plant management, foraging, and hunting (*57*). This subsistence pattern continued until increased trade and contact with outside groups (which occurred at variable times across the region, generally between 4000 and 500 years ago) precipitated the development of more intensive agriculture, and this pattern still survives in some areas today (for example, some Punan in the interior of Borneo) (*57*).

Although faunal accumulations from Niah Cave suggests that humans hunted orangutans and other arboreal animals as early as 45 ka ago (*39*, *40*), the technology required to effectively hunt arboreal game (specifically bone points used as projectiles for throwing spears or possibly bow and arrow) did not become widespread in Southeast Asia until around the Pleistocene/Holocene boundary (12 ka ago) (*58*). Significantly, the appearance of these artifacts often corresponds with an increase in the remains of arboreal mammals in fossil collections, suggesting a "change in hunting strategy to one favoring a greater dependency on arboreal game" [(*59*), p. 47]. For example, at Niah Cave, the terminal Pleistocene archeological remains include numerous hafted bone points and stingray spines that were components of light throwing spears or arrows (*59*), and this corresponds with a relative increase in arboreal primate specimens (including orangutans) in the faunal assemblage from about 15% of the total before 35 ka ago to 23 to 49% around the Pleistocene/Holocene boundary (*39*, *47*, *58*, *59*). The blowgun, which permits efficient hunting of arboreal prey over distances greater than 20 m and provides an even more effective way to hunt arboreal primates, probably appeared in Borneo only after 4 ka ago (*60*).

Fossil pollen and charcoal analyses of sites suggest that observable human modification of the environment in Southeast Asia also began, except in rare cases, around the Pleistocene/Holocene boundary (*46*, *54–57*). This modification took the form of forest burning and clearance to encourage the growth of particular plants and attract animals for hunting, with agriculture emerging much later in most areas (*57*). In Sumatra, there is palynological evidence of significant burning and land clearing by 11 ka ago and possibly as early as 18 ka ago (*54*, *57*, *61*). This roughly corresponds with the marked reduction in orangutan populations in Sumatra in the late Pleistocene or early Holocene, estimated at around 24 ka ago using genetic data (*27*). This decline, for which there are no detectable environmental triggers, has been attributed to human hunting (*27*). Sites in northern Borneo (Niah Cave and Loagan Buntut in Sarawak) show some evidence of small-scale forest clearing and management by the Pleistocene/Holocene boundary (in the case of Niah, possibly as early as 50 ka ago) (*39*, *46*, *57*), but these impacts appear to have been very localized and thus probably had minimal impact on orangutan populations. Evidence of widespread forest clearing and burning do not appear in Borneo until around 3 ka ago (*55–57*), and in general, human populations in Borneo's interior remained small and localized until iron tools, needed for larger-scale forest clearing and food production, began a slow (and incomplete) diffusion inland 1000 to 500 years ago (*56*, *62*, *63*). For example, people in the Kelabit Highlands in north-central Borneo were clearing land and cultivating sago 3 ka ago but did not begin large-scale forest clearing and rice cultivation until 450 years ago, corresponding with an increase in long-distance trade and the arrival of metal tools (*55*). This pattern of human environmental impacts in interior Borneo beginning ~3 ka ago and intensifying ~1000 to 500 years ago corresponds with the genetic evidence of a decline in Bornean orangutans between 2000 and 200 years ago (*41*, *42*). In summary, what we know of the regional timings of key human cultural changes (hunting innovations and significant environmental modification), when combined with genetic signatures of past orangutan population declines, appears consistent with the hypothesis that human activities, especially hunting, played a major role in decline in orangutans beginning around the late Pleistocene (Fig. 4).

The negative impact of human hunting on remaining orangutan populations probably increased during the colonial period, beginning in the 18th century (*10*, *25*). At this time, guns generally became more readily available, and the suppression of headhunting made travel and use of forested areas more feasible for local people, increasing hunting pressure in these areas. In some regions, orangutan skulls were sought as replacements for the human skulls that were no longer available for headhunting rituals (*64*). There is also documentation of the trade in live orangutans and orangutan body parts beginning at this time and historical commentary that remarks on the disappearance and range contractions of the orangutan in the 18th and 19th century (*10*). A recent analysis found that, since the colonial period, encounter rates with Bornean orangutans have dropped approximately sixfold (*65*). Given that this occurred even in areas with little forest disturbance and that there is no evidence to suggest alternative explanations (for example, disease), it is plausible that reduced densities in at least some populations of present-day orangutans are the result of hunting (*65*).

It is also possible that localized patterns of current orangutan distribution reflect human hunting. Orangutans are now absent from some of those forests in Borneo that appear ecologically suitable for orangutans but where nomadic hunter-gatherer populations (for example, Punan and Orang Ut) ranged in recent centuries (*66*, *67*). It
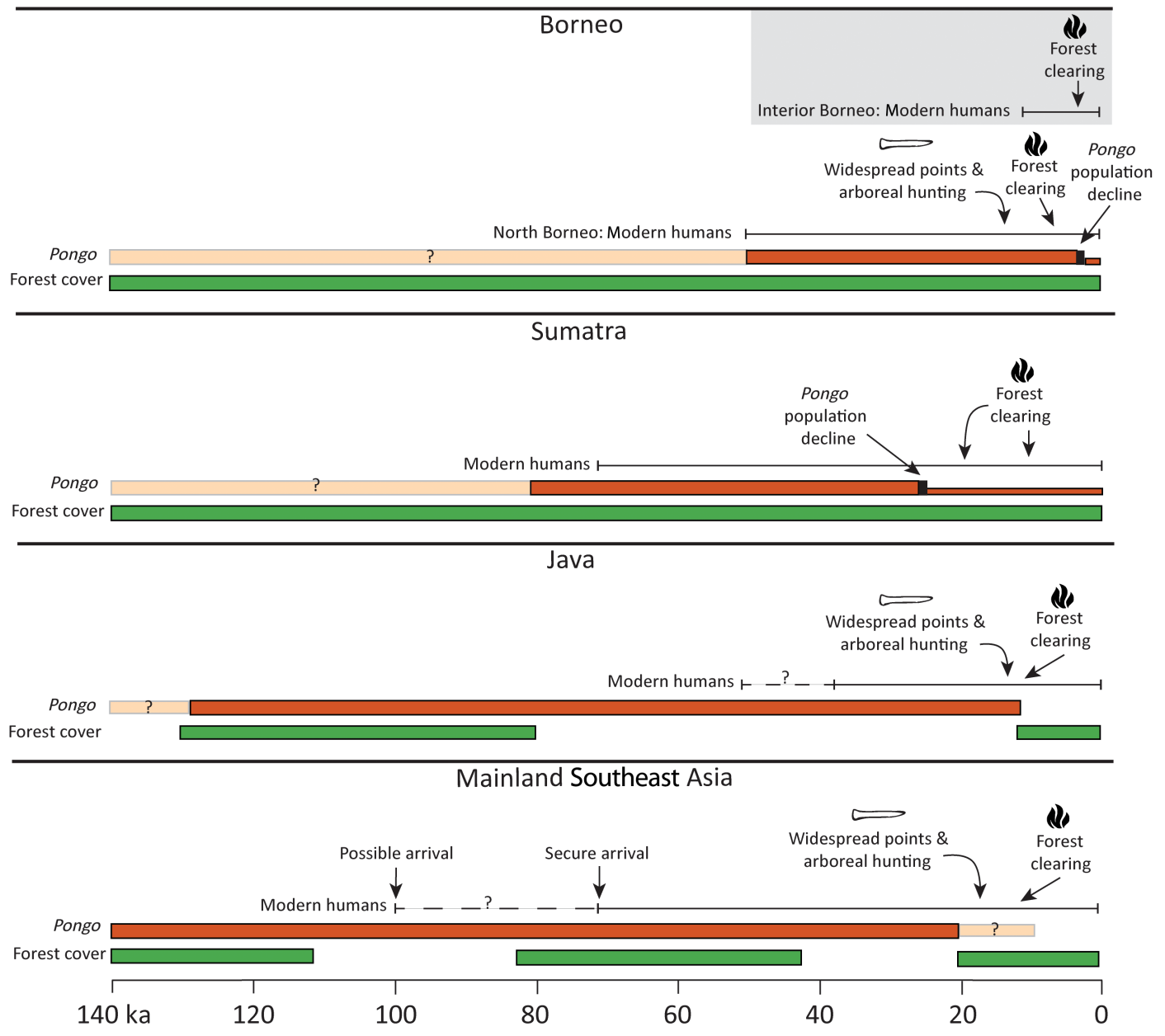
Fig. 4. Major ecological and human events and changes in orangutan distribution and abundance. The timing of orangutan disappearances or population reductions coincides with major changes in hunting technology and/or environmental modification. Open bars (for orangutans) or dashed lines (for modern humans) with question marks (?) represent possible periods of distribution or events that have not yet been confirmed through the fossil or archeological record. Interior Borneo and North Borneo are represented separately due to differing human histories.

appears that nomadic people living at low densities in interior forests and following wildlife wherever it occurs (68) likely had a greater impact on orangutans than settled farming communities (for example, rice-farming Dayak) who allocated less time to hunting and would have hunted primarily around their fields (69). Successful releases of ex-captive rehabilitant orangutans into these areas in Borneo (for example, the Bornean Orangutan Survival Foundation's Bukit Batikap release site in Central Borneo, which reports a cumulative 3-year survival rate for released individuals of 27 to 90%) (70) suggest that these forests may be ecologically capable of supporting orangutans, although

more time is needed to determine whether orangutans can survive in these forests over longer time frames. The survival of orangutans in these forests is consistent with the hypothesis that human hunting, rather than unsuitable habitats, is responsible for at least some modern localized orangutan absences. Furthermore, a recent large-scale analysis combining field survey data, predictive density distribution modeling, and remote sensing found that from 1999 to 2015, the largest number of Bornean orangutans were lost in primary and selectively logged forest (rather than heavily disturbed forest), with hunting being the most plausible reason for these losses (71). This also indicates

that hunting is an important factor influencing orangutan densities in relatively undisturbed forest.

A mixed hypothesis

The evidence suggests that human activity, especially hunting, was a significant factor in the decline in orangutan distribution and abundance after the late Pleistocene. The human impact hypothesis explains features of the fossil record that the environmental impact hypothesis cannot. However, the contribution of environmental factors to the late Pleistocene orangutan decline cannot be ruled out nor should it. We know that ecological factors influence orangutan populations today, and it is certain that significant environmental changes in the past also affected populations. A "mixed hypothesis," acknowledging both environmental and human impacts on orangutan populations in the past, appears to be the most satisfactory explanation. Perhaps environmental fluctuations throughout the Pleistocene resulted in sporadic reductions and fragmentation of orangutan populations when conditions were less favorable, but populations recovered and recombined when more favorable conditions returned. However, the confluence of environmental changes at the LGM, human-induced environmental modifications, and hunting may have resulted in orangutans disappearing from much of their range by the Pleistocene/Holocene boundary. These pressures may have also reduced the remaining orangutan populations in Borneo and Sumatra, resulting in the geographically restricted, generally low-density orangutan populations that we know today. Such a mixed hypothesis is also consistent with analyses showing that modern orangutan densities and distributions are better predicted by both environmental and human factors, especially hunting, than by either on its own (*49*, *71*, *72*). Given this interpretation, it seems that the evolutionary history of orangutans reflects the joint selective pressures of environmental factors and human activities.

APPLICATIONS AND WAY FORWARD

Implications for orangutan behavior

Understanding orangutan behavior and ecology requires regular reassessment and revision based on the best current evidence. Acknowledging the role humans have played in shaping orangutans in the past leads us to take a new look at factors that influence how we view their behavior now. Most of what we know of wild orangutan behavior is derived from observations spanning the last half-century from six long-term field sites covering a fraction of the orangutan's range (*73*). Recent reports of some populations regularly engaging in behaviors previously thought rare, such as moving on the ground (*74*), suggests that selection bias due to the limited number of study sites, differences in the extent of habituation, and differences in data collection techniques used by researchers have influenced our understanding of orangutan behavior. In addition, all long-term field sites have experienced some hunting and habitat disturbance and cannot be assumed to be unaffected by human activities (*73*). Recent studies of orangutans in modified landscapes are also expanding our knowledge of their behavioral flexibility and resilience (table S5) (*13*–*18*). Some populations persist in industrial oil palm and forestry plantations, although they depend on remnant natural forest for resting, nesting, and feeding, and the ability of plantations to support viable orangutan populations in the long term remains unknown (*15*–*17*). All beginning of sentence should read All this highlights the fact that our understanding of the breadth

of orangutan behavior and adaptability, especially the degree of flexibility present in feeding, locomotion, and social behavior, remains incomplete.

The purposeful movement of orangutans by humans can also influence behavior. As of 2013, at least 1500 orangutans were housed in sanctuaries as a consequence of habitat loss, confiscation from the illegal wildlife trade, and conflict with humans (*75*). An estimated 1000 rehabilitated orangutans were released from these facilities into either existing populations or empty habitats from 1964 to 2009, and ex-captives represent an estimated 2 to 3% of orangutans living free in native habitat (*76*). Orangutans are also translocated between sites as a result of habitat loss or conflict with humans (*77*). When resident orangutan populations exist in areas where these releases occur, these actions can potentially lead to alterations in local social organization and relationships, transference of learned behaviors, and the movement of pathogens, parasites, and genes between populations (*76*, *77*). Genetic variability among orangutan populations in Borneo and Sumatra indicates previous human-assisted transfers between populations and islands occurred in the recent and perhaps even the deep past (*78*). At Tanjung Puting National Park in Central Kalimantan, which houses one of the longest-running orangutan rehabilitation programs in Borneo, the release of orangutans of non-native subspecies in the 1970s to 1990s, as well as their subsequent interbreeding with native individuals, has been documented (*79*). These are not isolated incidents; although national and international laws require that orangutans be released into areas within the range of their own subspecies and where no extant orangutan population exists (*80*), enforcement and adherence to these regulations are inconsistent due to a lack of suitable release sites and difficulty in determining the provenance of some individuals (*79*). Despite the fact that it goes against existing regulations, the release of orangutans into areas where wild populations exist will likely increase in the future as habitat shrinks and the number of orangutans in rehabilitation facilities grows.

We make two recommendations to encourage a fuller understanding of the breadth of orangutan behavioral adaptations and how human activities have impacted them. First, to capture a more comprehensive picture of orangutan behavior and its environmental drivers, the research community should prioritize studies of orangutans living in contexts that are currently underrepresented in orangutan research (for example, inland hill and high-altitude forest, anthropogenic habitats, and even captive conditions that might mirror aspects of past higher-density conditions). A possible model for such an effort is the Pan African Programme (http://panafrican.eva.mpg.de), which aims to document the broad range of chimpanzee (*Pan troglodytes*) behavioral and cultural adaptations and their relationship to explanatory variables such as ecological conditions. This project expands the study of chimpanzees beyond a limited number of long-term study sites by relying on systematic sampling and technologies such as camera traps; similar methods could be followed for orangutans. Second, researchers should carefully document the history of human activities and current human impacts (including habitat disturbance, hunting, and orangutan translocations and releases) at all orangutan study sites and incorporate these as potential explanatory variables into analyses when appropriate. These data should be collected using standardized protocols to facilitate comparison across sites (*73*), as has been encouraged by the Orangutan Network (www.aim.uzh.ch/de/research/orangutannetwork.html) for studying other aspects of orangutan behavior and ecology.

Implications for orangutan conservation

The available evidence from studies of past and current populations indicates that orangutans are flexible enough to survive in a broad range of natural habitats and to persist in some human-modified areas, at least in the short term (13–18). In addition, the rate of forest cover change in Indonesia and Malaysia is among the highest in the world (81); more than 75% of orangutans in Indonesian Borneo live in areas open for development, including thousands of individuals in areas allocated to oil palm (82); around 35% of the remaining forest cover in Indonesia is found in industrial concessions (83); and modeling indicates that protected areas alone are insufficient to preserve Southeast Asia's biodiversity (84). These combined facts demonstrate the need and justification for a landscape approach to orangutan conservation that recognizes not only the vital importance of protected areas but also the conservation value of habitat outside these areas (Fig. 5). Landscape approaches work to maximize both biodiversity protection and human social and economic objectives in multifunctional areas that are subject to pressure from human activities (85). Some researchers and conservation organizations are currently using actions in keeping with this approach, for example, working with oil palm and other private sector stakeholders to prevent orangutan-human conflict and promote orangutan-friendly land-use policies (86), but this approach is not reflected in some prominent arenas that have significant influence on conservation strategy. An important example is Indonesia's latest Orangutan Action Plan (2007–2017), which represents official Indonesian government policy for orangutan conservation. Of the 74 specific actions aimed at conserving orangutans in this plan, the majority focus on creating and maintaining protected areas. Explicit attention to issues such as orangutan killings is found in only one action (1.4%), coexistence with people in three actions (4.1%), and multifunctional landscapes in seven actions (9.5%) (87). This "gap" between evidence and policy reflects the fact that conservation practice lags behind research (20, 21). Acknowledging the deeply intertwined history and present of humans and orangutans may help facilitate the shift from a paradigm of isolated islands of protection to one of broad coexistence.

The evidence demonstrates that a landscape approach to orangutan conservation must prioritize the prevention of killings and live capture and the maintenance of habitat connectivity (Fig. 5). Although orangutans appear to be adaptable to many human activities, it is clear that even low rates of killing and live capture can quickly decimate populations (48–51). Orangutans are primarily killed for food or as a result of conflict with humans, which arises when habitat loss and fragmentation force orangutans to use human-dominated areas where they exploit cultivated foods (50, 77, 88). Large-scale land clearing for industrial agriculture also creates opportunities for live capture for the wildlife trade, another significant threat to orangutan populations (89, 90). Indonesia has relatively strong laws and penalties for orangutan killing and capture, but these laws are poorly enforced because of a lack of financial resources, capacity, accountability, and incentives within government agencies (89, 90). Individuals who engage in orangutan killing or capture are rarely prosecuted, meaning that there is little disincentive for hunting or poaching (90). Recent highly publicized orangutan killings suggest that in some cases, industrial plantation management may encourage orangutan killing by employees to eliminate orangutans that are seen as pests (77). There may also be a lack of awareness of the illegality of these actions in some communities (88). An increase in penalties, increased funding for the government bodies responsible for investigating and responding to wildlife crime, rewards or incentives for reporting or prosecuting crimes, and campaigns to raise awareness of existing laws and change norms by decreasing the social acceptability of orangutan killings, which have been implemented in some areas, may help (89, 90). Anthropological study of the motives for orangutan killing
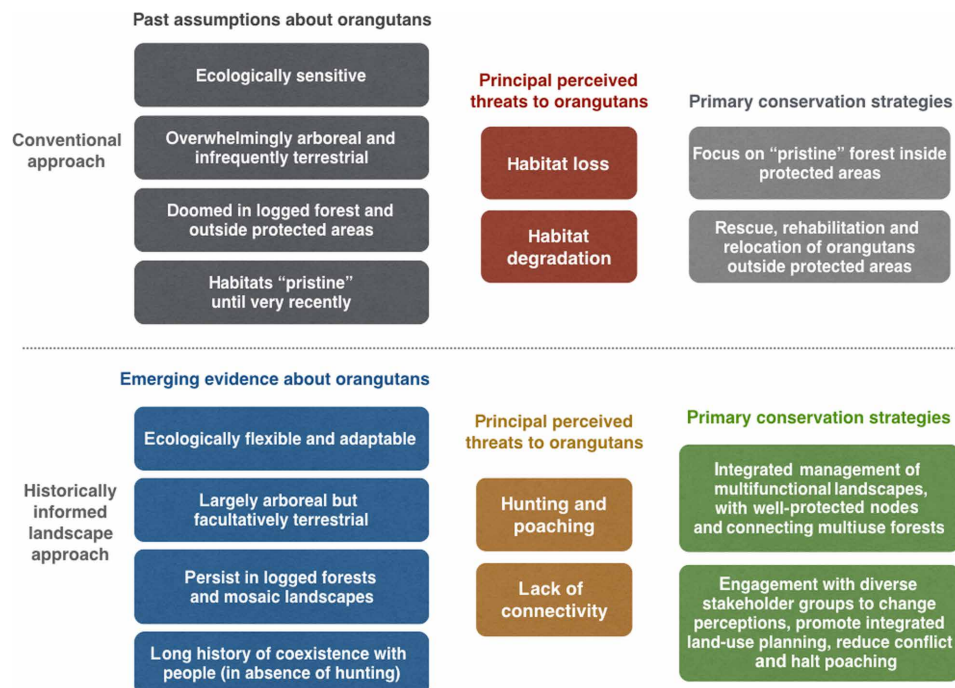

Fig. 5. Comparison of a more conventional approach to orangutan conservation with a historically informed landscape approach based on the latest evidence on orangutan history, adaptability, and the threat posed by killing and poaching.

is also important (*50*). In line with this, minimizing orangutan-human conflict is essential. Mitigation strategies, which have already been deployed successfully in some areas, can include deterrents to orangutans entering planted areas (for example, moats, nets, and noisemaking devices), planting low-risk crops that are less attractive to orangutans, compensatory payment for conflict, and education aimed at helping plantation management and farmers better understand orangutan behavior to avoid conflict (*77, 91*). Engagement with local communities and other stakeholders to determine what measures are most appropriate and feasible for them is a vital part of this process (*91, 92*). However, one of the best mitigation strategies is land-use planning and implementation that preserves natural forest areas and connectivity within multifunctional landscapes, minimizing the likelihood that orangutans will venture into areas of intensive human use to find food and shelter (*77, 91*).

Connectivity is essential to the long-term viability of orangutan populations living in multifunctional landscapes. Research demonstrates that orangutan activities in oil palm and forestry plantations are concentrated near areas of remaining natural forest (*16, 17*) and that orangutans must be able to move between patches of habitat to allow dispersal and maintain genetic diversity (*93*). Industrial plantations, mining, and small-holder agriculture represent the largest drivers of forest loss and fragmentation in orangutan range countries (*71, 81–83, 86, 94*), so initiatives to compel and incentivize orangutan-friendly policies by companies and communities should be a top priority. Current Indonesian law requires that industrial plantations retain 10% of natural forest in concessions (which can include degraded and regrowth vegetation) and requires the maintenance of corridors at least 100 m wide along all rivers and water bodies (*94*). These regulations, which are sometimes ignored, should be strictly enforced, but alone, they are not sufficient to support orangutan survival. In addition, planting native noncultivars in these remnant and regenerating forests could increase food and nesting sites for orangutans and other primates. These could include fast-growing trees such as *Mallotus* spp., *Neolamarckia cadamba*, *Nauclea* sp., and *Macaranga* sp., as well as keystone species such as *Ficus* spp. and other fruit trees that attract orangutans—but not people—and promote seed dissemination and forest regeneration (*94, 95*). At the landscape level, these remnant forests should be connected to larger, well-protected areas of natural forest with strategically placed corridors skirting planted forests, agroforests, and agricultural matrices that support economic development (Fig. 5) (*85, 86, 95*). This requires forward-thinking land-use planning in which appropriate forest patches and corridors are identified and set aside before any forest conversion, and these recommendations must be recognized and followed by all relevant land users. A crucial first step is the resolution of disagreements between government, private sector, and local communities over land-use rights and land tenure through projects such as the One Map initiative (https://sig-gis.com/projects/one-map-indonesia/) (*95*). Legal loopholes and perverse incentives that allow or even encourage forest clearing and poor land-use planning (for example, tax laws on timber revenue that encourage local governments and companies to develop plantations in areas of existing natural forest rather than degraded areas) should also be eliminated (*94, 95*). Finally, certification bodies (for example, the Roundtable on Sustainable Palm Oil) can play a role in incentivizing appropriate land-use planning and other orangutan-friendly behaviors by companies but are only effective if consumers demand certified products and if noncompliance has negative consequences (*94, 95*).

Successful implementation of these recommendations requires engagement and collaboration between a range of key stakeholders, including: government policymakers, local communities, scientists (who can provide expertise supporting or justifying policy or management strategies), nongovernmental organizations (NGOs) (who can develop capacity and provide support for pro-orangutan policy and behavior by governments, private industry, and communities), and the private sector. This collaboration is challenging and has yet to be broadly achieved. A major barrier is the lack of will to cooperate, which is driven, in our view, by the polarization of orangutan conservation that pits stakeholders against one another (for example, pro- and anti-palm oil) and obscures potential common ground. Initiatives and "boundary organizations" (*20*) that bring together key players around specific goals (for example, the recently formed PONGO Alliance, which connects private companies, NGOs, and scientists to promote orangutan conservation in oil palm plantations) could act as platforms to identify shared interests, build broad collaboration, and develop mechanisms to hold participants accountable.

Finally, we must also address current knowledge gaps that constrain our ability to effectively manage orangutan populations in modified landscapes. We have limited understanding of several key variables crucial to conservation planning, including what factors determine how orangutans use and move through different land-use types and the impact of population fragmentation, altered diets, changes in social structure, and increased human contact on orangutan reproduction and health. We must also assess variation in the ability of the different orangutan species and subspecies to adapt to human activities (*28, 30*) to determine how conservation strategies might differ for these populations. Finally, a landscape approach informed by the long common history of orangutans and people requires integrating a broad range of information and skills. Conservation scientists and practitioners must embrace interdisciplinarity, seeking insight from sociology, cultural anthropology, geography, archeology, paleontology, and other fields as appropriate.

Conservation in the Anthropocene

Dividing the world into natural and unnatural, as well as viewing humans as separate from nature, distorts our perceptions of nature and ourselves and hampers scientific understanding and conservation action (*96*). Despite nowhere being truly "pristine" (*2*), the urge to protect and mend "pristine nature" is still prominent in conservation (*97*). Accepting the prevalence of human influence does not mean abandoning efforts to protect the least human-modified ecosystems nor accepting human dominance of wild nature as an inevitability (*97*), but it does encourage a broader perspective that seeks to achieve conservation goals anywhere it can (*98*). It also encourages a more nuanced and evidence-based view of the relationship between humans and other species (*2–4, 99*) that encourages both pragmatic planning and opportunism to preserve biodiversity in a human-dominated future. The orangutan, shaped by its long shared history with people, can be an icon of this approach and its opportunities. Recognizing that this emblem of "untouched nature" is resilient and capable of adapting to some forms of human influence offers a new and more hopeful symbol for tropical conservation in the Anthropocene.

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