Introduction

Agro-industrial landscapes represent a significant and increasing part of the ranges occupied by apes in Africa and Asia. The changes caused by the transformation of the natural habitat of apes have profound impacts on food availability, activity patterns, natural dispersal and ranging patterns, social systems, exposure to new pathogens and risks linked to close proximity with people and infrastructure development (specifically roads). Suitable habitat for gorillas across central Africa has declined by approximately 30%–50% over the past two decades (Junker et al., 2012); this trend is likely to continue as various types of development expand in Africa. Indeed, approximately 43% of the area where African apes currently
occur is suitable for oil palm production and much of that is outside of protected areas, which translates into a real likelihood that current ape habitat will be converted to agriculture (Wich et al., 2014). Industrial-scale oil palm plantations have had well-documented, devastating effects on orangutan populations in Southeast Asia and could soon have a serious impact on African apes (Meijaard et al., 2011; Wich et al., 2012b).

Overall, forest clearance and degradation have a direct impact on all ape populations through habitat destruction and fragmentation. Logging and large-scale agricultural development also have indirect effects on these populations, specifically by facilitating access to previously remote areas, which can promote commercial wild meat hunting, including that of apes (Poulsen et al., 2009). Forest clearance tends to be accompanied by significant influxes of people into an area, which can expose apes to disease (Laurance et al., 2006; Leendertz et al., 2006b; Kondgen et al., 2008). Moreover, it can lead to further forest clearance across the landscape to sustain the newly established human populations (Cuaron, 2000; van Vliet et al., 2012).

All available evidence—especially what is known about the plight of apes in Southeast Asia—shows that agro-industrial plantations cannot sustain viable ape populations in the long term, even though there is increasing evidence that apes may be making use of agro-industrial plantations as supplemental food sources, sleeping sites or corridors in the short term (Ancrenaz et al., 2015). Apes use agricultural habitats primarily in the absence of an alternative, as their natural forest is cleared for agricultural and other uses.

To identify whether and how apes are using these different landscapes, and to assess whether that behavior can serve to promote ape conservation, it is essential to better understand how these newly created artificial landscapes impact apes and how they affect the interaction between people and apes. This information can then be used to formulate appropriate recommendations for regulating and overseeing bodies—such as governments, the Roundtable on Sustainable Palm Oil and industry—and to better engage agribusinesses, plantation owners and grower communities in managing these areas for more positive ape conservation outcomes.

There remains a dearth of information, knowledge and understanding of the real impact of agriculture-induced landscape transformations on ape ecology, adaptation and long-term survival. Much more is known about the impact on apes in Asia than in Africa, largely due to the greater intensity of industrial agriculture in Asia compared to Africa over the past few decades. Doubtless, the situation will change quickly in Africa, especially as large-scale oil palm production is expanding rapidly (RFUK, 2013; Wich et al., 2014). In Asia, more information is available for orangutans than for gibbons.

This chapter aims to provide an overall picture of the impact of industrial agriculture on ape ecology by summarizing formally published reports and gray literature; information gathered from experts, through discussion; and presenting the results of a 28-question online survey that was completed by the International Union for Conservation of Nature, the Species Survival Commission, and the Primate Specialist Group’s Sections on Great Apes and on Small Apes.

Key findings:

- Habitat conversion for agricultural purposes can result in the local extinction of ape populations either directly, through the destruction of ape habitat, or indirectly, by facilitating the killing, capture or starvation of apes.

- Habitat conversion to other types of land use, including industrial agriculture, has resulted in the decline of the range of orangutans and gibbons in Southeast Asia and is today a major driver of the decline of all ape populations. The conversion of
ape habitat is expected to accelerate in Africa, due in part to the expansion of industrial agriculture.

- Although great apes are able to enter agro-industrial landscapes to forage or disperse, they cannot survive in plantations alone and they need forest and natural habitat for their long-term survival.
- The survival of all apes is under serious threat unless 1) key habitats are taken into consideration in land use planning, 2) industry players and other stakeholders implement best management practices and 3) human communities that share the same habitat with apes tolerate this cohabitation. If we fail with any of these approaches, the future of all apes is seriously threatened.

**Different Crop Types: Different Impacts**

A variety of crops are grown in ape habitats. Cultivated fields range from small-scale cash crops to medium-sized mosaics of agroforest plantations—which produce crops such as banana, cashew, cloves, cocoa, coconut, coffee, corn, passion fruit, pepper, rice, sugarcane, sweet potato and tea—to commercial harvesting of agarwood (*Aquilaria* spp.) or pine trees, to extensive agro-industrial monocultures that cover tens or hundreds of thousands of hectares, for crops such as oil palm (*Elaeis guineensis*), sugarcane and tea, to industrial tree plantations.

In comparison to natural forests, agricultural landscapes have a simplified structure and composition: tree density and diversity are impoverished, the number of tree canopy layers is reduced (they lack the multi-dimensional characteristics of tropical forests that occur within 28 degrees north or south of the equator), and they present a uniform tree age structure with sparse undergrowth. In case of annual crops (crops harvested on a yearly basis, such as corn or rice), all canopy layers are completely absent. Depending on the type of crops cultivated, agricultural landscapes provide either a source of food for animals (mostly non-tree crops), or opportunities for shelter (non-edible tree crops) or both. Topsoil is leached or stripped by erosion or damaged by compaction, and microclimate conditions become drier and hotter (van Vliet et al., 2012). Impoverished ecosystems found in agro-industrial monocultures possess a far lower floral and faunal diversity than natural forest ecosystems. Plantation assemblages are typically dominated by a few abundant generalist species and invasive species that replace endemic and forest-specialist taxa (Fitzherbert et al., 2008).

Agricultural land is managed for the production of crops for humans and not for the maintenance of a diverse, natural ecosystem. Regeneration of these areas following the cessation of human exploitation requires intense management due to colonization by generalist and invasive species, with a very low likelihood for rapid and natural regeneration to the original forest composition. However, some ape species can temporarily use these altered landscapes as a food source, for nesting purposes or for travelling (whether for dispersing or ranging) between isolated patches of natural habitats.

**Different Ape Species: Different Impacts**

The current understanding of great ape ecology and behavior in agricultural and industrial landscapes is still very limited; much of the information comes from gray literature or anecdotal reports, although there is somewhat more research on orangutans (Meijaard et al., 2010; Campbell-Smith et al., 2011a, 2011b; Ancrenaz et al., 2015). Research on the impacts of agro-industrial
practices on gibbons and African great apes is urgently needed. Numerous variables interact to determine how well apes are able to survive in agricultural landscapes. These include the intensity and extent of agricultural operations; whether the plantation is a monoculture; the resident population’s former reliance on the converted area for keystone species or fallback foods; the degree of competition with sympatric taxa; and the severity of any additional anthropogenic impacts such as hunting, road access, human influx and associated agricultural expansion. It is therefore not surprising that clear themes on the impacts of large-scale agriculture on apes are difficult to isolate, especially given the large geographic range over which the different taxa occur.

In the long term, agro-industrial landscapes alone cannot sustain ape populations that are not connected to a larger metapopulation found in a more natural environment. It is important to remember that short-term survival of individual great apes cannot be equated with long-term success of a population. Indeed, research is needed to determine whether apes use landscapes that have been modified by human activity as part of their regular home range (by occasionally entering plantation areas), whether they are only transients in search of new forest habitat or whether they are taking part in a re-colonization process from nearby forests.

Orangutans

For a long time, scientists assumed that orangutans were very sensitive to forest disturbance (Rijksen and Meijaard, 1999; Delgado and van Schaik, 2000). However, recent studies have shown that orangutans are able to survive in exploited forests in Borneo and in a mosaic agroforest landscape in Sumatra (Ancrenaz et al., 2010; Campbell-Smith et al., 2011a, 2011b; Arcus Foundation, 2014). Recent surveys also show that orangutans have been found in large industrial acacia and oil palm plantations in Borneo (Meijaard et al., 2010; Ancrenaz et al., 2015). Given the drastically simplified structure of these agricultural landscapes, it is not surprising that the behavior and ecology of orangutans in these altered landscapes differ markedly from those in natural forests.

In the mosaic landscape of northern Sumatra, orangutans spend more time resting and less time feeding, as well as less time eating fruits and more time consuming bark; they also have a smaller home range than conspecifics in the forest (Campbell-Smith et al., 2011a, 2011b). This strategy, called “sit and wait”, is usually characteristic of periods of fruit scarcity, when orangutans rely heavily on substitute plant species to survive (Morrogh-Bernard et al., 2009). However, during a two-year study, natural fruits still contributed about 80% of their diet, suggesting that continued access to natural forest food sources is a strong determinant of the future of this population. In Kinabatangan, north Borneo, orangutans who are living in natural forests are regularly seen entering plantations and feeding on ripe fruits produced by mature palm trees and on young palm leaves (Ancrenaz et al., 2015).

In acacia and eucalyptus plantations, orangutans reportedly have longer daily travel distances than their wild counterparts.2 The duration of the daily period during which orangutans are active—the time between leaving a night nest in the morning and building a new one in the evening—has also been noted to have changed for those living in and around plantations; they remain active later into the night to exploit plantation crops after humans have left (Campbell-Smith et al., 2011b; Ancrenaz et al., 2015). These patterns are similar to those of other crop-raiding non-human primate species in Africa and Asia (Krief et al., 2014). Orangutan nests can also be found in acacia and eucalyptus trees and in mature oil palms when no other trees are available for nesting (Meijaard et al., 2010; Ancrenaz et al., 2015).
Gibbons

Although gibbons do occur in forest patches within agricultural matrices, the consensus among questionnaire respondents is that gibbons do not generally use industrial landscapes as sleeping sites or as main sources of food; in particular, unlike the other apes, gibbons do not consume pith. Nor are gibbons normally targeted directly by humans in human–wildlife conflict over crop raiding, as perceptions of gibbons are generally positive; however, they do fall victim to hunting and the pet trade, as discussed below.

The impacts of agriculture on gibbons are somewhat difficult to assess as there are very few studies focusing on gibbons in an agricultural landscape. Due to their territorial and strictly arboreal nature, gibbons may be more affected by the immediate impacts of agricultural regimes than many other wildlife species (Asquith, 1995; Kakati, 2004). Specifically, the expansion of industrial agriculture affects gibbons by fragmenting their habitat and, in some cases, by clearing all the trees from a plantation (Vasudev and Fletcher, 2015). A lack of connectivity in the forest limits accessibility for immigration and emigration into an area, which affects dispersal from birth groups; it can also restrict ranges, reduce access to food, heighten territorial competition, increase isolation and restrict the gene pool.

Gorillas

Western and eastern gorillas—also known as lowland gorillas—are typically found at higher densities in secondary forests than in primary forest (Bermejo, 1999; Rogers et al., 2004; Head et al., 2012), which is likely linked to their reliance on understory vegetation. Gorillas have been observed in abandoned plantations, probably also because of the greater abundance of herbaceous vegetation in these forest clearings (Tutin, 1996). The two locations where mountain gorillas
live, Bwindi Impenetrable National Park, Uganda and the Virunga Massif of Rwanda, Uganda, and the Democratic Republic of Congo (DRC), are currently protected by national park status, which presumably buffers their habitat against industrial agriculture, but these areas are small and the gorillas do exit the national parks to crop raid. While little is known about Grauer’s (eastern) gorillas, it is clear that they inhabit large areas of unprotected forest interspersed with human settlements, so they are likely impacted by agriculture. Both western and eastern gorillas, including mountain gorillas, are hesitant to cross roads, but they may venture more than half a kilometer outside of forests when areas of their former range have been removed.

Little is currently known about how gorillas respond to habitat changes brought on by agricultural landscapes. This knowledge gap mainly reflects the fact that there are relatively few industrial agricultural landscapes in areas occupied by gorillas, but the need for research is great as agricultural expansion in Africa is expected to increase dramatically in the foreseeable future (Wich et al., 2014). Few systematic studies have been done; among them are investigations of crop raiding on small-scale subsistence farms by mountain gorillas. This research reveals that gorillas consume many crops, but primarily banana plants (the pith, but not the fruit), eucalyptus bark, pine tree bark and, occasionally, coffee, corn, passion fruit and sweet potatoes (Kalpers et al., 2010; Fairet, 2012; Seiler and Robbins, 2015).

Chimpanzees and Bonobos

In general, there is limited understanding as to how chimpanzees and bonobos manage in degraded or mono-dominant landscapes and what factors may compromise their survival and their ability to adapt to rapidly changing landscapes, such as those typically imposed by industrialized agriculture. Nevertheless, it is evident that such landscapes may raise the frequency of encounters between apes and people; threaten ape survival and habitat; and challenge coexistence between people and apes locally. The risks vary across species, however. While the bonobo range across Africa is mainly restricted to the south of the Congo River in the DRC, in areas dominated by forest (IUCN and ICCN, 2012), chimpanzees inhabit a wider array of habitat types that range from primary forests to savannah, woodland and fallow, to agriculture-dominated landscapes across areas of West, Central and East Africa (Oates et al., 2008b).

Chimpanzees are indeed highly flexible in their behavior and can readily adapt to mixed agroforest landscapes with small-scale farming by foraging on crops, travelling along human paths and crossing roads to access different areas of their range (Hockings, Anderson and Matsuzawa, 2006; Hockings, 2007; Hockings and Humle, 2009). However, more research is required to determine whether and how such landscapes are able to sustain chimpanzees in the long term. Crop foraging potentially favors chimpanzee survival in such landscapes, as it provides the apes with dense clusters of highly nutritious foods. Wild chimpanzees have been reported to consume as many as 51 different parts from 36 different species of cultivars across their range (Hockings and McLennan, 2012). However, some crops with commercial value, such as banana, cacao, corn, mango, oil palm, papaya, pineapple and sugarcane, have been identified as “high-conflict” crops—that is, people are less tolerant of apes when they eat or damage these high-value crop types. Another study finds that chimpanzee communities that faced high levels of disturbance to their home ranges also experienced greater levels of harassment from people (Wilson et al., 2014b). Such situations run the risk of exacerbating retaliatory killings or the
capture of apes (Brncic et al., 2010). For an example of this, see Case Study 1.2 in Chapter 1 (page 29).

Although some bonobo populations are known to forage in secondary vegetation alongside agricultural fields (J. Thompson, personal communication, 2014), these apes tend to avoid areas of high human activity and fragmented forest, and the presence of humans significantly reduces effective bonobo habitat (Hickey et al., 2013). Bonobos may also consume banana, palm pith, pineapple and sugarcane, but their crop consumption remains less studied than that of chimpanzees (Hockings and Humle, 2009; Furuichi et al., 2012; Georgiev et al., 2013); research may be limited simply because many bonobo populations occur in more remote areas dominated by primary forest, with relatively low human densities and levels of activity (UCN and ICCN, 2012). As seen with chimpanzees, bonobo reliance on commercial (and subsistence) crops for food and nesting is likely to increase with the expansion of primary forests loss, land conversion and habitat fragmentation (Dupain and Van Elsacker, 2001; Myers Thompson, 2001); however, the extent of these changes will depend primarily on the type of crops grown locally.

The impact of industrial agriculture is of growing concern with respect to the status of both chimpanzees and bonobos across their ranges—be it linked to new developments or to the reclamation or reactivation of historical plantations of crops such as oil palm, rubber or sugar (see Box 6.1). In African countries whose conditions are propitious to oil palm and other large-scale agricultural development—such as Angola, the DRC, Gabon, Ghana, Ivory Coast, Liberia, the Republic of Congo and Sierra Leone—more than two-thirds of the land suitable for oil palm development is located outside protected areas and overlaps with great ape habitat (Wich et al., 2014). Many of these areas, especially across West Africa, already represent degraded landscapes, where chimpanzees, in particular, have been thriving for generations, ironically, it seems, thanks to human tolerance and the presence of wild oil palms, which may be a key species for some chimpanzee communities, as they serve both nutritional and nesting purposes (Humle and Matsuzawa, 2004; Leciak, Hladik and Hladik, 2005; Brncic et al., 2010; Sousa et al., 2011).

In areas where wild oil palms persist, it remains unclear whether chimpanzees or bonobos would significantly target commercially grown palms, even if they knew the oil

---

**BOX 6.1**

**Reclamation of Abandoned Plantations: Impact on Bonobos and Chimpanzees**

In the DRC, many commercial plantations—whose crops include banana, cassava (also known as manioc and tapioca), coffee, oil palm, quinine, root crops, rubber, sugarcane, tea and tobacco—date back to the early 20th century and colonial times. Although most are located outside the bonobo range and have remained dormant as a result of decades of military and political insecurity, international companies, such as Feronia Inc., are now increasingly reclaiming abandoned oil palm, rubber and sugarcane plantations and reviving the commercial industry (J. Thompson, personal communication, 2014). Some of the areas they have targeted are within the bonobo range, such as those in Equateur province and along the Congo River. Although the large distances and the lack of overland infrastructure have greatly limited and concentrated plantation locations in specific areas, the probability of a rejuvenated industry looms on the horizon (FAO, 2012a); the risk of expansion into more pristine forest areas is thus high.

A similar pattern is apparent in Nigeria, especially in Cross River state, a key area for the Nigeria–Cameroon chimpanzee. Rural transformation in Cross River state is driven by the privatization of defunct plantations and the crowding out of smallholder production systems by agricultural investors (Schoneveld, 2014b).

Across three of Feronia’s reclaimed oil palm concession areas in the DRC, road infrastructure increased by 34% in less than three years between 2011 and 2013 (Feronia, 2014). A rubber plantation has recently been reactivated in the DRC’s Luo Scientific Reserve, which is part of the bonobos’ current natural range (T. Furuichi, personal communication, 2014). However, there is no evidence to date to suggest that the Wamba bonobos use rubber trees for food or nesting, nor do they seem to use coffee or oil palm, which also occur in the area; what is known is that bonobos forage locally on subsistence and cash crops (Furuichi et al., 2012).

The main concern for the apes in these landscapes is habitat loss and degradation, as well as increased hunting as plantations are reactivated and road infrastructure is expanded.
palm as a resource (Humle and Matsuzawa, 2004; Hockings and Humle, 2009); if they did, the risk of “conflict” with plantation owners would certainly be heightened. Their behavior may ultimately depend on what other natural resources are available to them across the seasons, as crop consumption, at least for chimpanzees, is often inversely correlated with the availability of natural foods in their habitat (Hockings, Anderson and Matsuzawa, 2009). Nesting patterns are also likely to depend on what other suitable species are available.

Although oil palm development is not as much of a concern in East Africa, other developments, such as sugarcane, pose a potential threat to apes and their habitat.

The Varying Impacts of Different Phases of Production

Infrastructure Development

The development of agro-industrial plantations has resulted in increased remodeling and fragmentation of the natural habitat and ape populations. Examples include the removal of trees that border small tributaries and the digging out of drains and trenches, both of which create new barriers that are impassable to apes as none of the ape species can swim. This process of fragmentation will further threaten ape survival unless natural or artificial connection bridges are constructed (Ancrenaz, Dabek and O’Neil, 2007; Das et al., 2009). Other infrastructure development, including roads, train tracks, electricity cables, human settlements and fences, also make the landscape less navigable for wildlife.

Where forest is fragmented, apes may be forced to travel on the ground to cross to different fragments due to the loss of canopy continuity, or because of isolation, such as if families or individuals are stranded in a small number of trees. Increased time on the ground makes the apes, and particularly gibbons, vulnerable to predation. Fragmentation can also lead to malnutrition and increased parasite loads in the medium term, and population decline in the long term (Das et al., 2009).

In Central Africa and in Indonesia, the decline in ape densities has been linked to the growing number of roads and human settlements (Kuehl et al., 2009; Marshall et al., 2009b). This correlation largely reflects an increase in hunting for wild meat and the pet trade, as areas become more accessible to subsistence and commercial hunters, and transportation from remote areas to major cities becomes easier (Wilkie and Carpenter, 1999; Wilkie et al., 2000; Poulsen et al., 2009).

Wild apes, including those habituated to human presence, are likely to behave cautiously when close to human landscape features such as crop fields or roads. The effects of road infrastructure on forest composition and structure depend on road network density, width, spatial layout and traffic intensity (Malcolm and Ray, 2000; Wilkie et al., 2000; Blake, 2002). Although secondary roads may be smaller and less frequented than primary transport roads, the former may occur at higher densities within the landscape and thus represent an impediment to natural patterns of habitat utilization in apes.

Chimpanzees are known to be more nervous and are more vigilant when entering crop fields to forage than when they are in the forest; they also stay closer together when crossing roads, especially wider ones (Hockings, Anderson and Matsuzawa, 2006, 2012). Recent observations in the Kinabatangan, on the island of Borneo, showed that wild habituated orangutans who were followed both inside and outside the forest were more wary of the presence of observers and more difficult to follow in oil
palm landscapes (F. Oram, personal communication, 2014).

In the long term, the fragmentation and isolation of ape communities, groups and populations that result from significant landscape changes made for infrastructure development are likely to cause genetic in-breeding, which would significantly impact population viability. The heightened presence and activities of humans may also act as deterrents to dispersal and further erode the genetic health of the local population. Among chimpanzees, young adolescent females resident in less disturbed areas may be dissuaded from immigrating into semi-isolated communities if these exhibit high rates of encounters between humans and apes, thus further impacting the long-term survival of such communities (Matsuzawa, Humle and Sugiyama, 2011).

Habitat Destruction and Clearance

In most cases, the development of industrial crops involves the removal and conversion of natural forest, whether primary or already disturbed (Wilcove and Koh, 2010; Gaveau et al., 2014). Overall, the impact of forest conversion on ape populations is dramatic for all species, and it should be stressed that populations that survive the initial forest conversion stage continue to decline after the establishment of the plantations (Bruford et al., 2010). Nevertheless, some differences across taxa are expected when the natural habitat of apes is converted to industrial crops.

**Orangutans:** Forest clearance has the worst impact on the long-term survival of orangutan populations. Genetic studies in Kinabatangan, on the island of Borneo, show that 95% of the original orangutan population was lost over the past 200 years; that decline can be attributed to human activities, mostly hunting and forest clearance for oil palm development and other crops (Goossens et al., 2006). Forest conversion results in the death of nearly all resident and territorial orangutans—namely adult females and flanged males—either through direct killing and open-burning practices, or as a result of starvation (Rijksen and Meijaard, 1999). However, non-territorial, unflanged adult male orangutans can move away from disturbed areas and take refuge in undisturbed areas (MacKinnon, 1972; Ancrenaz et al., 2010); the result is a transitional “excess” of males in remaining forest patches (Bruford et al., 2010).

**Gibbons:** Undisturbed gibbon groups change and expand their territories as part of their natural behavior, suggesting that they may be able to move to avoid human disturbance such as forest clearance (O’Brien et al., 2003; Cheyne, 2008a, 2010; Fan Peng-Fei and Jiang Xue-Long, 2008; Savini, Boesch and Reichard, 2008; Kim, Lappan and Choe, 2010). However, there are limits to the distance a group can move and to available forest for establishing new territories, depending on the level of disturbance and the number of groups affected; that is, a small number of groups may be able to move, yet the carrying capacity of the destination forest area may soon be reached (Akers, Islam and Nijman, 2013). If a group cannot establish a new territory, the most likely outcome is a breakup of the group or the death of an adult. The surviving adults and offspring may be unable to defend the territory, leading to group breakdown, reduced reproductive opportunities and possibly the associated deaths of the remaining group members (Choudhury, 1991; Kakati, 2004; Savini et al., 2008; Cheyne, 2010; Cheyne, Thompson and Chivers, 2013).

**Gorillas:** The loss of nearly all naturally occurring vegetation renders habitat unsuitable for gorillas. To date, no studies have been conducted on the impact of large-scale clearing on gorillas, but in all likelihood it...
would result in the death by starvation of the majority of the individuals if there are no remaining forest fragments or nearby areas of intact forest in which the apes can seek refuge. Small-scale subsistence farming can involve the clearance of the majority of native plant species, but some trees and understory plants may remain. If such plants are present and the area borders on intact forest, gorillas are likely to continue to attempt to forage in this area if it previously constituted a part of their home range, particularly if they are habituated for tourism or research purposes (Kalpers et al., 2010).

**Chimpanzees and bonobos:** Extensive clearing can cause a decline in chimpanzee density and shifts in their home range, as evidenced by large-scale clearance conducted as part of commercial logging activities (Johns and Skorupa, 1987; Chapman and Lambert, 2000; Chapman et al., 2000; Morgan and Sanz, 2007). The ramifications can include severe social disruption, as a result of increased competition, conflict and stress, with potential long-term consequences for the reproductive and general health of the population (White and Tutin, 2001; Emery Thompson et al., 2007a; Kahlenberg et al., 2008). Similar patterns are expected among the bonobos, although related data are more limited.

**Young Plantations**

In a mosaic landscape or close to the border between natural habitat and agro-industrial crops, animals who live in nearby forests or remaining forest patches are prone to using newly established plantations, especially...
during periods of fruit scarcity in the forests. The likelihood of foraging on young plantations increases with the crops’ proximity to the apes and depends on the type of crop.

In mosaic habitats, small forest patches, isolated trees or edge areas may still attract apes into plantations for feeding, even if they do not make regular use of these plantations. When forest patches are not producing food, some individuals tend to enter plantations to feed on resources that are available to them to survive. Orangutans typically feed on fruits cultivated by smallholders and cambium of acacias and other trees (Salafsky, 1993; Yuwono et al., 2007); gibbons eat young leaves of acacia or the petiole (growing tip) of agarwood trees (S. Spehar, personal communication, 2014; U. H. Reichard, personal communication, 2014); chimpanzees and bonobos are known to pull out young fronds of wild oil palms for consumption of the petiole, making it likely that knowledgeable individuals might perform a similar foraging behavior if exposed to young saplings of commercially selected and grown oil palms or other plant species (Humle and Matsuzawa, 2004; Hockings and Humle, 2009).

The impact of young plantations on gorillas is unknown. Their response would likely depend on whether the understory or the ground vegetation is kept clear or if plants eaten by the gorillas are able to regrow. For example, herbaceous vegetation consumed by gorillas can grow in both young tea plantations and stands of eucalyptus trees (Kalpers et al., 2010; Seiler and Robbins, 2015). As gorillas are unlikely to feed on the seedlings of eucalyptus or tea, this should not directly impact these crops.
Animals can cause significant economic losses on newly established plantations (Ancrenaz et al., 2007; Campbell-Smith et al., 2011b). Many of them are either killed or captured and translocated to other places (Hockings and Humle, 2009).

**Mature Plantations**

As with recently cleared areas and young plantations, the impact of mature plantations on apes depends on the planted crops, the management of the plantations and the presence of nearby forest patches.

**Orangutans:** Over time, orangutans who live in forests that are close to industrial plantations start to use mature plantations for dispersal, as a supplementary source of food or for nesting. As orangutans are mostly arboreal, it is no surprise that all age and sex classes have been recorded roaming and dispersing in acacia, eucalyptus and other tree species plantations (Chung et al., 2007; Meijaard et al., 2010). However, recent studies in Kinabatangan show that orangutans are also found in mature oil palm landscapes (Ancrenaz et al., 2015). The animals bend and break large fronds to build their nests in the central part of the plant (Ancrenaz et al., 2015). Orangutans who venture into oil palm plantations feed on young shoots and ripe fruit of mature oil palm plants, which they pick from bunches on the ground or take directly off the palm.

Recent fieldwork and surveys in the Kinabatangan floodplain reveal that these activities had no negative impact on the fruit productivity of the mature palms (Ancrenaz et al., 2015). As a result, orangutans are not considered a major pest for mature oil palms (those that are at least five years old), although they can inflict significant damage when the plants are younger, as discussed above. In Kinabatangan, the vast majority of orangutan signs were found within 50 m of forest patches, suggesting that they are reluctant to disperse in oil palm plantations, as has already been documented on Sumatra (Campbell-Smith et al., 2011a). In this landscape, orangutans often walk on the ground to travel faster and to avoid detection (Ancrenaz et al., 2014, 2015).

In industrial tree plantations, orangutans eat tree bark of acacias (Chung et al., 2007; Meijaard et al., 2010). In eastern Kalimantan, acacia plantations established close to Kutai National Park suffered a tree mortality rate of 5%–10% because of bark stripping by orangutans (Meijaard et al., 2010).

**Gibbons:** Much of the focus of gibbon studies has been on tree plantations and little is known about the impact of low-level plantations, such as cocoa, rice and sugar-cane. Gibbons are predominantly arboreal, much more so than the larger apes. While gibbons can walk bipedally for short distances, they are not likely to cross areas that are devoid of trees or covered by mature palms. Consequently, gibbons are not seen in areas of low-level crops, where there are no trees. Such plantations likely act as barriers to gibbon movement. Gibbons have not been shown to inhabit oil palm plantations, although they are sometimes present in isolated patches of forest left within a plantation. They do not consume the oil palm fruit or the pith of the young leaves. Gibbons may, however, enter acacia plantations and consume leaves (S. Spehar, personal communication, 2014). It is possible that mature plantations, even ones with trees, act as a barrier to dispersal; there is a need for more studies on the presence of gibbons, as no information is currently available on their long-term persistence in plantations, nor on their impact on mature plantations of any type.

**Gorillas:** Plantation management—which involves either the clearing of herbaceous understory vegetation that is consumed by gorillas, or tolerance of its growth among the crops—and the presence of nearby intact forest determine how mature plantations affect gorillas. Certain crops—such as banana and eucalyptus trees, which
are highly sought after by gorillas—may in fact attract the apes as they reach more advanced stages of maturity (Seiler and Robbins, 2015).

**Chimpanzees and bonobos:** To date, there is no evidence that either chimpanzees or bonobos can thrive in mature plantations. While more research and reporting is urgently required, it may be assumed that their survival depends on the availability of other vegetation types and forested habitats within the landscape, human attitudes, pressures and density; another factor is the extent to which apes can use crops as a resource, such as mango, oil palm, oranges, pineapple and sugarcane. If chimpanzees have knowledge of the oil palm as a resource, the crop could potentially help them meet most of their nutritional needs. In some areas, chimpanzees are known to consume the rich oily fruit and the kernel of the nut throughout their range, using natural stone or wooden objects to crack open the hard-shelled nut. They also eat the tip end of young fronds, the pith of mature fronds, and potentially the oil palm heart and beetle larvae contained in the dead trunk of the palm (Humle and Matsuzawa, 2004). The oil palm can also act as a highly preferred nesting species for chimpanzees in areas where oil palms are relatively abundant in the landscape, as in Guinea and Guinea-Bissau (Humle, 2003; Sousa et al., 2011). In Guinea, for example, Bossou chimpanzees spent nearly one-quarter of their feeding time consuming wild or feral oil palm parts; they also preferentially nest in wild or feral oil palms, especially at night (Humle, 2003; Soumah, Humle and Matsuzawa, 2014).

As yet, there is no indication that chimpanzee nesting or foraging on wild or feral oil palms has any significant impact on oil palm survival or fruit productivity (Humle and Matsuzawa, 2004; Soumah et al., 2014). However, this may depend on which part is preferentially consumed; consumption of oil palm flowers could, for instance, severely impact oil palm production and the frequency of use could affect palm survival over time (Soumah et al., 2014). However, when chimpanzees consume oil palm fruit, they often ingest the seed, which is then evacuated whole in the feces, a favorable environment for sapling growth (Lambert, 1998; Humle and Matsuzawa, 2004). Chimpanzees can also disperse the seeds of other crop species such as cacao, mandarins and oranges, thus promoting the growth and the distribution of these high-value species (Lambert, 1998; Hockings and Matsuzawa, 2014).

**Conclusions on the Impacts of Different Phases of Production**

As discussed, the different phases of agricultural development and production have variable impacts on ape populations. Forest conversion has the most negative impact on the short-term survival of the animals—through habitat loss, destruction of natural food sources and an increased rate of killing. By using newly established plantations, apes who survive forest conversion can cause significant economic losses and conflicts with people, which can lead to retaliatory killings. As crops mature, the extent of conflict may decrease significantly, partly due to the reduced ape population density in the area. At some stage, these plantations may simply act as “corridor” areas between fragmented forest patches, as long as the apes’ ability to travel in these planted landscapes is not impeded and is tolerated by workers and plantation owners.

**Remediation**

**Set-aside versus Total Clearance**

As discussed, current information suggests that agro-industrial plantations cannot sustain viable orangutan populations in the long term (Meijaard et al., 2010; Ancrenaz et al.,...
2014); this conclusion is likely the case for all ape species. However, these landscapes could at least provide essential connectivity between populations in areas of natural forest (Wich et al., 2012b); they could also maintain some basic ecosystem functionality (Wilson et al., 2007a; Koh and Wilcove, 2008a; McShea et al., 2009; Meijaard et al., 2010; Ancrenaz et al., 2015; Mendenhall et al., 2014).

A conservation paradigm for apes in an agro-industrial landscape must include the preservation or restoration of small patches of forest—a system known as “set-aside”—as opposed to the total clearance of forest. Used as corridors or stepping stones, these forest patches—even if degraded—play an important role in sustaining ape populations by providing dispersal, nesting or food resources. All remaining forests and forest patches located within an industrial landscape should be identified as high conservation value forests (HCVF) and should be maintained as natural forests. Indeed, retaining forests within an agro-industrial landscape is the key to maintaining ecosystem functionality, because it ensures the viability of meta-populations of many wildlife species by facilitating dispersal and survival (Maddox et al., 2007; McShea et al., 2009).

Challenges to Rehabilitating Agricultural Lands

Deforested areas are very challenging environments for the natural growth of seeds and seedlings. The underlying soil or peat has been damaged and eroded; its nutrients have been depleted; the soil and water tables and waterways have often been polluted with artificial chemicals; the ground layer is open, compacted and exposed to a high amount of sunlight; much of the area is exposed or flooded during the wet season; forest soil seed stocks have been destroyed; and seed dispersal into the area is low. These problems are particularly severe in peatlands, which suffer from additional impacts of disruption to natural hydrology and subsequent increased fire risk when converted (Page et al., 2009).

Natural regeneration in these areas is often very slow, with much of the land colonized by sedges, rushes and low-growing shrubs, which are generalist or invasive species that can provide a barrier to subsequent secondary succession. The overall focus needs to be on assisted regeneration, including identifying species that would be suitable for large-scale reforestation projects. These species should be able to grow quickly to form a closed canopy, thus creating shade to make the habitat more hospitable to other tree species, and attracting seed-dispersing fauna to the area. This helps to speed up the rate of natural (unassisted) regeneration and, in the long term, to re-establish a forest that resembles its original state. Young secondary forest habitats resulting from a regeneration process can provide important fallback foods for bonobos (Hashimoto et al., 1998; Terada et al., 2015); they can also act as an essential source of food and nesting species for chimpanzees in modified landscapes (Humle and Matsuzawa, 2004; N. Bryson-Morrison and T. Matsuzawa, personal communication, 2015).

In the past, many reforestation projects have concentrated on commercial tree species or have adopted methods that are expensive—such as the use of fertilizer—or labor-intensive. Resources for most conservation projects are generally quite restricted, and therefore high costs are likely to reduce the scope and scale of planting. High-intervention projects are also less transferable to other sites, so any lessons learned are of less value to the conservation community. Therefore, a clear focus should be placed on identifying species that are naturally suited to growing in these conditions, and that require as little human intervention as possible (Matsuzawa et al., 2011; OuTrop, 2013). As these reforestation activities usually
occur decades after a plantation begins operation, a clear long-term plan and commitment is needed from agro-industrial companies.

It is important to stress that reforestation is a very lengthy and expensive exercise. In every case, it is always more economical to avoid cutting down the forest than to initiate a reforestation program after damage caused as a consequence of poor land use planning.

Long-term Impacts

Ongoing population fragmentation, especially outside of protected areas, is a major issue for most ape populations in Asia and in Africa. Habitat fragmentation following agricultural development leads the original meta-population to be split into a number of smaller subpopulations, as has been the case among Cross River gorillas (Bergl et al., 2008). These small populations become more vulnerable to genetic drift and inbreeding, and unpredictable events triggered by climate changes or anthropogenic pressures (Shimada et al., 2004; Bergl et al., 2008; Xue et al., 2015).

When forests are transformed into non-forest landscapes without adequate large-scale land use planning, which would include provisions for the survival and population connectivity of apes and other wildlife, the impact on the original biodiversity in general and resident ape populations in particular is devastating. Many designated high conservation value areas are too small or too isolated from other forests to be viable long-term habitats for apes. When forests are replaced with crops, most animals disappear, as described above. The compression effect—meaning the compaction of the habitat available to wildlife, which is sometimes referred to as the “crowding effect”—occurs when animals are exposed to disturbance in part of their range and thus start to use their home range differently; that is, they increase the use of parts that have not been affected.
Habitat loss is therefore expected to result in the compression of groups into undisturbed areas or “refuges” (Shimada et al., 2004; Bergl et al., 2008).

Most ape species present some degree of range overlap: male and female orangutans; family groups of gibbons, with estimates ranging from 11% to 64%; gorilla groups; and chimpanzee or bonobo communities (Idani, 1990; Reichard and Sommer, 1997; Singleton and van Schaik, 2001; Wrangham et al., 2007; Bartlett, 2008; Cheyne, 2010; Robbins, 2010; Furuichi, 2011; Nakamura et al., 2013). After the cessation of logging activities and other disturbances, individuals may return to their former range if some forest or other suitable habitat still remains (MacKinnon, 1971; Johns and Skorupa, 1987); however, there is great variation across the species and among individuals.

If crowding occurs for a short period of time or during periods of high seasonal fruit abundance, many animals may survive agricultural development in the short term. For chimpanzees, however, the situation is risky as they face a high risk of aggressive encounters with members of neighboring communities (Wrangham et al., 2007); within a community, such compression could also result in heightened levels of competition and aggression among females (Miller et al., 2014). In comparison, bonobos are more tolerant of neighboring groups (Furuichi, 2011).

If the crowding is long term and the compressed population exceeds the carrying capacity of the habitat, members of the resident population, as well as the displaced apes, run the risk of starvation.
male bias in any given dispersing generation. This situation would result in more males than available females, an imbalance that prevents many males from forming a new group with a female. Limited information is available about genetic relatedness among wild gibbon populations, but the available data suggest that the level of relatedness is naturally high (Liu et al., 1989; Reichard and Barelli, 2008; Zhou et al., 2008; Reichard, 2009; Kenyon et al., 2011). The impacts of forest loss, population compression and reduction into fragments can thus be expected to have a long-term influence on the genetic viability of an affected population.

**Gorillas**

In case of compaction, gorilla groups that arrive in an area that is already occupied by another group or groups will face serious social and ecological challenges. Males compete intensely for females, both by retaining female group members and by attempting to get more females to join their group. Loss of habitat, which leads to greater crowding of individuals in a particular area, would likely result in higher rates of intergroup interactions and increased aggression among adult males. In turn, this could cause an increase in adult male mortality. The death of the dominant male of a one-male group of gorillas can also result in infanticide of unweaned infants, who are still dependent on milk, by other adult males, meaning that increased mortality among adult males has far-reaching consequences for other age and sex classes and group stability (Robbins and Robbins, 2004; Robbins et al., 2013).

The ability of gorillas to move through a matrix of subsistence farming or industrial agriculture, which has implications for their ability to disperse as well as for genetic diversity, depends largely on the distance between suitable forest patches. However, the ability to retain connectivity between patches, as well as the level of genetic diversity within and between patches, depends on more than absolute distance, as dispersal patterns differ for males and females. Female gorillas always disperse directly between social units and do not travel on their own, but males disperse alone and travel greater distances (Yamagiwa, Kahekwa and Basabose, 2003; Harcourt and Stewart, 2007; Guschnsiki et al., 2009; Arandjelovic et al., 2014; Roy et al., 2014a). As a result, males may have more of an impact on gene flow within populations and among isolated subpopulations (Bergl et al., 2008; Guschnsiki et al., 2009; Roy et al., 2014a). Human disturbance is believed to have resulted in an abrupt reduction not only in population size, but also in genetic diversity in Cross River gorillas, emphasizing that the impacts of altered landscapes are far more complex than only having fewer apes (Bergl and Vigilant, 2007; Bergl et al., 2008).

**Chimpanzees and Bonobos**

As a result of habitat compression and increased home range overlap between neighboring communities, chimpanzees are likely to commit intercommunity lethal attacks on both adults and infants (Watts et al., 2006; Williams et al., 2008; Wilson et al., 2014b); however, such events are unlikely to arise among bonobos, among whom records of conspecific killings remain extremely rare (Wilson et al., 2014b). If forced into areas dominated by agricultural crops, chimpanzees may have to forage on crops to meet their nutritional needs (Hockings et al., 2009). They may also become more visible—though not necessarily more habituated—to local people, thereby potentially exacerbating people’s fear of chimpanzees and heightening the risk of retaliation from farmers or plantation workers (Hockings and Humle, 2009). All these factors necessarily imply increased competition and stress.
BOX 6.2
The Road to Extinction: The Bossou Chimpanzees in Guinea, West Africa

The Bossou chimpanzee community in southeast Guinea, West Africa, lives about 6 km from the Nimba Mountains, which are home to several chimpanzee communities. This group inhabits an agroforest matrix and is semi-isolated from its neighbors. Research shows that the community is likely to become extinct. The threats to their survival include the following:

- A lack of immigrant females;
- The disappearance of natal females (that is, over the years, as expected, some of the younger females may have emigrated from the community, possibly to join neighboring communities in Nimba, although this assumption remains unconfirmed);
- The aging of its members (some are over 50, and older females no longer reproduce) (Sugiyama and Fujita, 2011); and
- Sporadic mortality events associated with outbreaks of respiratory infection predominantly affecting infants and older individuals (Humle, 2011a).

It may be too risky for females from other communities in the Nimba Mountains to travel through an open savannah or agricultural forest matrix from their more contiguous and pristine natal primary forest. These Nimba females are much more likely to disperse to known neighboring communities along the massif than to immigrate into a community exposed to high levels of human presence and disturbance, whose existence is potentially unknown to them, such as Bossou.

It is ironic that—in spite of the evident risk of extinction of this community, as associated with longer-term cumulative genetic erosion, reproductive senescence and respiratory epidemics—until recently, Bossou chimpanzees showed significantly shorter interbirth intervals and higher infant survival rates than conspecifics more dependent on wild foods for their survival (Sugiyama and Fujita, 2011); this pattern was attributed to their significant reliance on highly nutritious crops available to them in their habitat. However, the chimpanzees at Bossou also have an extremely diverse diet comprising more than 200 plant species, which represent 30% of all available plant species in their heterogeneous environment (Humle, 2011b). While rapid habitat conversion, especially on a large scale, can have significant negative effects on the reproductive success and survival of individual apes and populations, feeding on crops may, in some cases, actually benefit the reproductive success of particular populations in the short term, provided there is no retaliation from people and the landscape is a mixed agricultural forest mosaic that enables dietary diversity, rather than one dominated by monocultures.

This example highlights the heightened vulnerability to epidemic outbreaks of small gregarious groups of apes and the importance of ensuring gene flow between groups or subpopulations and maintaining a landscape propitious to dispersal.

Conclusions on Long-term Impacts

In all likelihood, the transformation of natural forest to non-forest landscapes results in increased physiological and ecological impacts on apes and other wildlife, including increased densities of apes and other wild species or shifts in activity patterns, such as nighttime crop raiding (Krief et al., 2014). Increased densities of apes and other wildlife could also imply increased risk of parasitic infection and ill health, thus exposing the community or population to added risk (Gillespie and Chapman, 2006).
stressors that impact the short- and long-term survival of ape populations. The decline of food resources has a negative impact on breeding success—such as ovarian function and overall reproductive success and survival rates (Knott, 1999; Knott, Emery Thompson and Wich, 2009). It increases inter- and intra-group competition for resource access and, in some cases, inter group or inter-individual aggression. Stress also affects the immune system and general health of the animals (Muehlenbein and Bribiescas, 2005). In addition, habitat fragmentation and any associated barriers to natural dispersal are likely to hinder gene flow and contribute to the reproductive senescence of these populations (see Box 6.2). Combined, these factors can lead to a negative growth rate, to a decline in overall population size and, ultimately, to local extinction.

The Impact of Socio-economic and Cultural Values on the Forest–Agriculture Interface

Human presence is greater in agricultural lands than in natural forests; a hectare (0.01 km²) of industrial oil palm plantation sees human presence 56 days per year, on average (Ginoga et al., 2002). This presence introduces new risks and challenges for surviving wildlife, such as emerging diseases, more frequent encounters and conflicts with domestic animals and people, and, consequently, more frequent killings of apes and other wildlife. The survival of viable populations of apes and other wildlife in heavily transformed landscapes ultimately depends on the general perception of human communities that share the same environment.

The public perception and acceptance of wildlife reflect a complex combination of factors. These are frequently related to economy: is wildlife perceived as a source of loss because of conflicts or a source of gain through ecotourism and other services? Or are wild animals valued for other reasons, such as an individual appreciation of an animal’s proximity for recreation, the place of animals in traditional culture and folklore, and awareness of their role in maintaining health of the ecosystem (Meijaard et al., 2013)?

The presence of wildlife in newly created human-made (anthropogenic) landscapes, such as agricultural lands, often results in crop-raiding activities and an increase in conflicts. These conflicts lead to emotional distress and occasionally to significant economic losses (Nepal and Weber, 1995; Ancrenaz et al., 2007; Chung et al., 2007; Campbell-Smith et al., 2011b, 2012). Worse, the occurrence of conflicts creates a negative perception of wildlife and becomes a major impediment to building local support for conservation (Webber, Hill and Reynolds, 2007; Marchal and Hill, 2009; Aharikundira and Tweheyo, 2011; Campbell-Smith et al., 2012; Gore and Kahler, 2012).

Successfully addressing conflicts between wildlife and humans requires the design and implementation of technical solutions that decrease or suppress the damage (Hockings and Humle, 2009). For a strategy to yield long-term success, however, it also needs to integrate the underlying social and stakeholder dimensions of the problem (Ancrenaz et al., 2007; Dickman, 2010, 2012).

Human–Ape Interactions

Agriculture Development and Crop-raiding Activities

Apes who are living within or close to plantations can cause substantial damage to people’s crops, as discussed above. Orangutans, for example, kill acacia trees by stripping bark and cambium (Meijaard et al., 2010); they also pull out stems and destroy young palms
to feed on the heart of the plant (Yuwono et al., 2007). In addition, they can consume entire fruit crops in orchards that belong to local villagers (Campbell-Smith et al., 2011b); in this case, orangutan crop-raiding activities are better explained by the presence of ripe cultivated fruits than the scarcity of wild fruit. Most of the raiding activities take place less than 500 m from forest edges (Ancrenaz et al., 2015). Gibbons have not been identified as a major crop-raiding species and are generally not subjected to retribution killings. Studies have reported the presence of subsistence foods and crops, such as cloves, coconut, rattan, sago, sweet potato and taro, around gibbon habitat, but the local gibbons did not use any of them (PHPA, 1995; Quinten et al., 2014; gibbon experts, personal communication, 2014).

In Africa, studies in Bwindi, Uganda indicate that crop raiding by gorillas appears to be primarily influenced by the presence of palatable crops or native species growing in the understory of eucalyptus, pine and tea plantations—and not by food availability within the park (Seiler and Robbins, 2015). In Kibale National Park, which is also in Uganda, forest-dwelling wildlife, including chimpanzees, are more likely to forage on crops in fields located within 500 m of the forest edge than further afield (Naughton-Treves, 1997, 1998). Chimpanzees, in particular, can be responsible for significant damage (Hockings and McLennan, 2013).

Disease Risk

Diseases can play a significant role in the decline and extinction of apes and other wildlife (Leendertz et al., 2006a). The occurrence of emerging infectious diseases is also a major threat to global public health, with high economic impacts. These diseases result from complex demographic and anthropogenic environmental changes, including global climate change, urbanization, increased presence and incursions of people in natural ecosystems, international travel and trade, land use change and agricultural intensification, poaching for wild meat and the live animal trade, and the breakdown of public health (Daszak et al., 2013). The increased risk of disease transmission between humans and apes who live in human-modified landscapes originates from physical proximity between humans and apes and associated elevated levels of stress that could impede an individual’s immune system from combating disease and infection (Muehlenbein and Bribiescas, 2005).

In the case of Asian apes (orangutans and gibbons), increased terrestrial locomotion in a human-made matrix increases the susceptibility to contamination with pathogens of human origin (H.B. Hilser, personal communication, 2011; Ancrenaz et al., 2014). In general, the current state of knowledge on pathogens and diseases of wild orangutans and gibbons is limited, except for some studies on intestinal parasites (Mul et al., 2007; Labes et al., 2010). Therefore, the epidemiology and dynamics of emerging diseases that could potentially affect these species in human-made landscapes need to be investigated (Gillespie and Chapman, 2006; Travis et al., 2008; Muehlenbein and Ancrenaz, 2009).

Disease transmission is a major threat to gorilla and chimpanzee populations across sub-Saharan Africa (Köndgen et al., 2008). Less is known about bonobos, but their susceptibility to diseases is expected to be similar to that of chimpanzees.

Chimpanzees and gorillas are prone to a variety of diseases, including Ebola and a range of typically human-borne diseases ranging from pneumonia to polio (Formenty et al., 2003). All African apes are particularly vulnerable to respiratory disease outbreaks, especially where regular and close proximity to humans is prevalent (Sakamaki, Mulavwa and Furuichi, 2009; Humle, 2011a; Palacios et al., 2011).
There is also strong evidence that chimpanzees and gorillas harbor greater parasite loads and share several types of intestinal parasites with humans in areas occupied and disturbed by people (Rwego et al., 2008; McLennan and Huffman, 2012). One study suggests that increased ecological overlap may promote microbial exchange between chimpanzees and humans (Goldberg et al., 2007); since some bacteria are pathogenic—meaning that they can induce illness—and infections can sometimes be fatal (such as Escherichia coli), this study stresses the value of strategies aimed at limiting inter-mixing of gastro-intestinal bacteria in order to benefit both human health and ape conservation.

Intense exploitation and heavy human presence in agricultural landscapes that are used by apes definitely increases the risk of disease transmission between taxa. It is vital, therefore, to promote good sanitary and health standards of people living near ape populations, and to implement a thorough health monitoring program of the wild populations that are in close contact with humans. Failure to do so can have catastrophic consequences (König et al., 2008; Humle, 2011a; Reed et al., 2014).

Retribution Killings

In most places where apes cause damage, people are resentful and can be very upset by crop-raiding animals foraging in their fields. In some areas of Borneo, subsistence farmers consider orangutans the most damaging crop-raiders (Hockings and Humle, 2009); in many human-modified landscapes, killing the “pest” animals is often seen as the ultimate solution to conflicts with orangutans (Davis et al., 2013; Abram et al., 2015). The effects of industrial agriculture on African great apes are still mostly unknown, but the likely impacts can be estimated based on those of small-scale subsistence farming. In places where raiding is not tolerated or people fear great apes, they are chased off, injured by snares and other devices, or killed in retribution (Brncic et al., 2010; Kalpers et al., 2010; Fairet, 2012).

Foraging in planted fields, plantations or orchards is potentially high-risk behavior for all species of apes (Hockings et al., 2009). Consequently, animals may shift their active period and enter the crops in the early morning or late afternoon, when people are not around (Ancrenaz et al., 2015; Krief et al., 2014). In most of the chimpanzee range in Africa, adult males tend to be the ones who forage on crops, since they are more likely to exhibit risk-taking behavior than are adult females or subadults (Hockings, 2007; Wilson, Hauser and Wrangham, 2007b).

It should be noted that retaliatory killings are not the only way that apes who live close to plantations are killed. Indeed, recent interview surveys conducted in Kalimantan, the Indonesian part of Borneo, reveal that animals were also killed for a number of other reasons, including the illegal trade in meat, pets and traditional medicine, as well as due to fear and ignorance. Research has identified a complex interplay of variables that predict the risk of orangutans being killed at the local level; among these, religion is the prime indicator and Christian people are the most likely to kill orangutans (Davis et al., 2013; Abram et al., 2015). These surveys also concluded that between 2,000 and 3,000 orangutans have been killed every year over the past three to four decades in Kalimantan (Meijaard et al., 2011); the rate is well above what the species can sustain (Marshall, 2009). These findings indicate that many orangutan populations will go extinct within a human lifetime (60 years) if killing continues at the current rate (Meijaard et al., 2012). In some regions of Africa, wild meat hunting represents a major threat to ape populations and also fuels the pet trade, since infants are also often captured as a by-product of such activities (Tutin et al., 2001; Poulsen et al., 2009; Ghobrial et al., 2010).
The Need for Better Land Use Planning

The best way to limit the negative impacts of agricultural and industrial development on wild ape populations is to prevent any large-scale development where major ape populations occur. When all or part of the range of an ape population is designated for land conversion, it is crucial to undertake a sound and precise land use planning program that considers the needs of apes (and other wildlife) before any new development takes place. HCVF and other important unprotected forest patches, as well as corridors, have to be identified, marked and set aside at the earliest stages of land use planning (Ancrenaz et al., 2015). It is also essential to evaluate the entire landscape structure and to incorporate other types of land use in proximity to plantations to minimize fragmentation and the potential exacerbation of conflict with ape species that are likely to forage on commercially grown or subsistence crops. In addition, management plans that try to use connectivity between forest fragments as a strategy need to consider not only the distance between forest patches (structural connectivity), but also the quality of the area between the patches and the level of human activity within connecting areas (functional connectivity) (Kindlmann and Burel, 2008).

In addition, a zero-tolerance policy on the killing of apes and other harmful acts needs to be enforced at all management levels in agro-industrial plantations. The opening of ape habitat for oil palm and other plantations increases conflicts between humans and apes across their range, and allows increased access to poach apes for the pet trade and for wild meat. The killing of apes—either as a retaliatory means to protect people’s crops or for meat—has a knock-on effect on reproductive success and significantly affects the long-term survival of ape populations. Indeed, studies have shown that orangutan populations cannot withstand annual killing rates of more than 1% of reproductive adults without going extinct (Marshall et al., 2009b). This is linked to the fact that apes exhibit a slow reproductive rate, as a result of long interbirth intervals and slow maturation of youngsters to adulthood (Williamson et al., 2013).
Photo: The opening of ape habitat for oil palm and other plantations increases conflicts between humans and apes across their range, and allows increased access to poach apes for the pet trade and for wild meat. Severed gorilla feet and hands await further smoking on a rack to be placed over a fire. This is a common method used for preserving wild meat, allowing suppliers enough time to get the product to market. © Jabruson, 2015. All Rights Reserved. www.jabruson.photoshelter.com

Conclusions on the Need to Incorporate the Human Social Dimension in the General Picture

More information is urgently required on the drivers and patterns of crop foraging in apes, the impact of humans on their social, foraging and ranging behavior, and the drivers and extent of killings for all species, whether retributive or for meat, in anthropogenic landscapes.

Human–ape conflict leads to emotional distress in apes and occasionally to significant economic losses for humans (Nepal and Weber, 1995; Chung et al., 2007; Campbell-Smith et al., 2012). The occurrence of conflict
creates a negative perception toward wildlife and becomes a major impediment to building local support for conservation (Webber et al., 2007; Marchal and Hill, 2009; Campbell-Smith et al., 2012; Gore and Kahler, 2012). The successful mitigation of conflict between apes and humans requires the design and implementation of technical solutions that decrease or suppress the damage done to both sides (Hockings and Humle, 2009). But for a strategy to yield long-term results, it also needs to integrate the underlying social and stakeholder dimensions to the problem (Dickman, 2010). There is thus an urgent need to disentangle the real from the perceived cost of ape foraging on crops, and to assess the socioeconomic and political dimensions of conflict among local stakeholders that could have an impact on ape survival.

As the needs and aspirations of local communities are the ultimate drivers of conservation successes or failures outside protected forests, it is clear that they should be encouraged and assisted in order to become engaged actors in—and not only beneficiaries of—conservation efforts (Steinmetz, Chutipong and Seuaturien, 2006; Meijaard et al., 2012).

### Survey Results: Summary of Main Impacts

Following the International Primatological Society meeting in Vietnam in August 2014, the authors of this chapter developed a questionnaire using the online survey tool SurveyMonkey. The main purpose was to

---

**TABLE 6.1**

Impact of Industrial Agriculture on Apes and Ape Use of Crops Based on Questionnaire Responses and Expert Opinions

<table>
<thead>
<tr>
<th>Ape species</th>
<th>Bonobos</th>
<th>Chimpanzees</th>
<th>Gibbons</th>
<th>Gorillas</th>
<th>Orangutans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of respondents</td>
<td>2</td>
<td>9</td>
<td>17</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Countries represented</td>
<td>DRC</td>
<td>Guinea-Bissau, Republic of Congo, Tanzania, Uganda</td>
<td>Bangladesh, China, India, Indonesia, Malaysia, Thailand</td>
<td>Republic of Congo</td>
<td>Indonesia, Malaysia</td>
</tr>
<tr>
<td>Apes are known to forage on commercial crops</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Apes are known to nest in some plantation tree species or oil palm</td>
<td>Unknown</td>
<td>Yes</td>
<td>Not available</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Ape habitat loss reported as a result of agro-industry – in the last 10 years</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Increased habitat fragmentation occurring – in the last 10 years</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Plantations result in a decrease in the apes’ natural foods – in the last 10 years</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>Shift in ape range and ranging patterns – in the last 10 years</td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Increased ape–human interaction – in the last 10 years</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td>Increased number of ape rescue interventions – in the last 10 years</td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
</tbody>
</table>
how flexible is ape ecology and life history? What can be learned from comparing ape populations in intact versus disturbed areas? How much of their diet comes from plantation crops, and how much from wild foods found in secondary forest patches?

- Have apes drastically changed their energy budgets to accommodate the change in environment? If so, are the adapted budgets sustainable in the long term?

- Is the use of landscapes gendered? Are females using small areas, or are they moving between secondary forest patches? Do males have different patterns?

- What is preventing apes from surviving long term in fragments?

- Is normal dispersal taking place in any fragmented habitats?

### Ape population and home range sizes

- What are the population sizes of apes in modified landscapes?

- What are the minimum requirements of species-specific home ranges, including tree and feeding tree densities? To what extent do home ranges fluctuate over time?

- How can ape populations be maintained, helped to recover or reintroduced in protected areas in mosaic agricultural landscapes?

- What are the carrying capacities of plantations?

- Endocrinological studies would allow for analysis of ape energy budgets and stress levels, and how these factors affect reproductive capacity.

- What is the effect of habitat compression in the remaining forest on the natural socioecology of apes?

- The collection of demographic information could inform population viability analyses and other modeling.
Mitigation of negative human–wildlife interactions

- What is the frequency of interactions, conflict and killings between apes and people?

Land use planning

- How can land use planning be improved?
- How can habitat be secured and corridors established?

Conclusions

A significant part of the current range occupied by apes will be profoundly transformed by agriculture within the next decades, as range countries intensify their commercial agricultural activities to bolster their economies and to address the needs and demands of the growing human population.

Scientists alone will not change how the world evolves or how human development progresses. There is, however, an urgent need for the results of research to reach stakeholders beyond academic circles—to ensure that all social groups are informed: politicians, local communities, private industry, the media, civil society and others. To reach a wider audience, multi-disciplinary engagement is required (Johns, 2005; Meijaard et al., 2012).

The future of apes—and of many other species—very much depends on the long-term security of strictly protected forests and already established agroforest matrices where illegal logging, natural resource extraction and poaching are efficiently controlled and where ape populations are large enough to cope with potential catastrophic events, such as fires and disease (Meijaard et al., 2011). These forests must have the ecological gradients that contain key resources to ensure that apes are able to adapt to climate change (Gregory et al., 2012). Across wider
landscapes, scientifically based, regional land use planning is needed to delineate the zones of interaction around protected forests or important forest patches for apes and their surroundings, which also provide irreplaceable hydrological, ecological and socioeconomic services to people (DeFries et al., 2010).

Ideally, these core forest areas should remain connected with other forests, which could potentially be used for commercial timber extraction. Indeed, well-managed timber concessions result in significantly lower levels of forest conversion than those associated with industrialized agricultural activities (Gaveau et al., 2012, 2013); this finding highlights the possible value of the timber industry in maintaining ape populations in the long term (Arcus Foundation, 2014). Some agricultural companies already have certain attributes that are useful for biodiversity conservation: well-trained staff, significant financial resources, and clear and strong operation protocols for managing their activities. Therefore, it is urgent to engage with these stakeholders to improve their practices.

Natural forest areas could also be buffered by low-intensity plantations such as acacia, pulp and paper, and other mosaic industrial tree plantations (McShea et al., 2009). These landscapes could then be connected to high-intensity use areas, such as other agro-industrial schemes and areas where infrastructures, roads and small-scale agriculture dominate alongside human settlements (Wich et al., 2012b).

The design of such dynamic landscapes must be approached across the whole landscape rather than at the site or species level (Morrison et al., 2009; Sayer et al., 2013). The focus needs to be shifted from conserving specific sites and species to respecting landscapes and processes; that shift involves envisioning a larger-scale landscape approach. The resulting ecological benefits
extend far beyond just apes. Conserving ecosystem functions and services can only happen if environmental concerns are considered at the beginning of the planning process. The best chance of achieving this goal requires full engagement from and collaboration among scientists, NGOs, government agencies and the private sector (Doak et al., 2014).

Regardless, it is inevitable that agro-industrial landscapes will have a predominantly negative impact on apes. In newly created agro-industrial landscapes, the long-term impact of human disturbance on biodiversity is strongly influenced by the general configuration of the landscape after habitat loss and alteration (Fischer and Lindenmayer, 2006; Forman, 2006; Hilty et al., 2006). While apes may be able to modify their behavioral ecology by incorporating plantation crops into their diet, little is known about their long-term adaptability to human-created landscapes, the long-term impacts of industrial agriculture and the loss of biodiversity and ecosystems. What remains abundantly clear is that apes depend on natural vegetation, which is normally incompatible with large-scale plantations. More research is needed to understand the most effective strategies for conserving apes in a human-modified landscape. It is therefore imperative to investigate whether and how industrial-scale agricultural landscapes can serve the conservation of apes and biodiversity. At the same time, it is important to ensure that agricultural landscapes retain some functional ecological role to guarantee a minimum level of ecosystem services (Foster et al., 2011).

**Endnotes**

1. Industrial tree plantations grow timber species such as *Acacia* spp., *Eucalyptus* spp., *Albizia* spp. (silk tree), *Hevea brasiliensis* (rubber tree) and *Neolamarckia cadamba* (known as Kadam or Laran).

2. S. Spehar, unpublished data, reviewed by the authors.

3. To get to the oil palm heart, chimpanzees reportedly use a modified frond as a pestle; this behavior is known as “pestle pounding” and has been recorded in Bossou, southeast Guinea, and less frequently elsewhere (Ohashi, 2015).

**Acknowledgments**

Principal authors: Marc Ancrenaz, Susan M. Cheyne, Tatyana Humle and Martha M. Robbins

Reviewers: Takeshi Furuichi, Mark E. Harrison, Andrew J. Marshall and Melissa Emery Thompson