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Habitat Modelling of the Amur Leopard and Siberian Tiger for Future Reintroduction. Using Conservation Priority Setting, Ecological Corridors and Carrying Capacities

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Habitat Modelling of the Amur Leopard and Siberian Tiger for Future Reintroduction. Using Conservation Priority Setting, Ecological Corridors and Carrying Capacities

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Contents

Abstract

Both the Siberian tiger (*Panthera tigris*) and the Amur leopard (*Panthera Pardus*) are under threat by increasing anthropogenic induced impacts. These have reduced both populations to only a fraction of their former numbers and distributions. Many know believe that reintroductions may represent the best way to save these sympatric predators from extinction. Using known locations of both species, along with what we considered to be the three key drivers of their habitat selection, prey presence, human impact and competition, suitability models were computed. These determined potential suitable habitat for each species, being the first to include the entirety of both species' historic distributions. Regions were revealed, for each of the species, that could act as an area for reintroduction and conservation prioritizing. A total of 29,666km^2 of suitable habitat was identified for the Siberian tiger, split into 25 areas (Further split into 4 regions). 22,116km^2 of suitable habitat was discovered for the Amur leopard, which would take their range to over 34,000km^2. For the Amur leopard, 18 areas were identified, which were further split into 4 regions. Each of these regions was then critically analysed using conservation prioritizing, the key drivers and suitability values leaving a single respective region for each of the Siberian tiger and Amur leopard. A region of 9,149km^2 stretching across the Jilin-DPR Korea border, was selected as that of highest suitability for the Amur leopard. Carrying capacity estimates for the region suggests this will increase the Amur leopard population by 89 breeding adults, which almost doubles the wild population. For the Siberian tiger 13,967km^2 of suitable habitat was identified across the Primorski Krai-Heilongjiang border with carrying capacity estimating habitat for 50 breeding adult Siberian tigers. Least-cost path analysis was used to find potential corridors between each of these suggested areas and the current wild populations, preventing fragmentation of these reintroduced populations. To limit the anthropogenic impacts that have previously, and currently, damaged wild populations, conversations with local people and educating them about the importance of these predators for biodiversity will help to make these reintroductions a success. This suitability model and following discussions add to the growing reintroduction planning process and offers new insight for suitable regions. These continuing efforts are vital for successfully reintroducing the Amur leopard and Siberian tiger.

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Chapter One: Introduction and Review of the Literature

1.1 Large Carnivore Ecology

1.1.1 Ecological Roles of Carnivores

In the early 1900s, ecologist Charles Elton began to recognise how various carnivores regulate populations of the underlying prey species (Elton, 1927; Beschta and Ripple, 2009). Following on from this, the role a predator has within an ecosystem was further investigated. The swift increase in deer populations across the United States of America after the loss of their key predators, the wolf and cougar (*Puma concolor*), led Leopold *et al* (1947) to conclude that it was these predators absence, that caused the irruption of deer. This is one of the first descriptions and observations of a trophic cascade (Leopold *et al*., 1947). It wasn't until a study by Paine (1980), investigating marine food webs and the effect a species of starfish, *Pisaster ochraceus*, has upon a prey species of mussel, *Mytilus californianus*, that the term 'trophic cascade' was coined. It is now recognised that these controls are what influence the strength of ecosystem functioning (Ripple *et al*., 2014). This kind of ecological interaction has since been recorded in many ecosystems around the world, the loss of a predator having effects that ramify throughout the trophic levels.

The effect that a loss of top order predators can have on the underlying trophic levels is illustrated in Ghana. A survey undertaken in the 1960s found high densities of ungulates and primates within the country's six savannah parks, along with 8 species of large carnivore (Brashares *et al*., 2001). However, human persecution of these large carnivores persisted over the next half of the century with many killed out of fear or in retaliation for taking livestock. A repeat of the survey in 2004 discovered a significant population decrease in the four largest carnivores. In the 1969 survey, these predators had an average of 348 detections per month. The 2004 survey only averaged 31 detections per month (Brashares *et al*., 2010). These large carnivores also became extinct in three parks by 2004 and in the parks where they still resided, their range had substantially contracted (Brasheres *et al*., 2010). The lack of large carnivores in these parks resulted in a change across the trophic levels. The olive baboon (*Papio anubis*) increased in observations by 365% with a documented range increase greater than 500% (Brashares, 2010). As a result of this, a population decrease in both small monkeys and ungulates was found. A change in feeding behaviour of the baboons is also noted in the absence of predation, with them becoming heavily dependent on livestock and crops (Brashares *et al*., 2010). This too creates drastic changes across the ecosystem.

Perhaps the most well known and documented example of a trophic cascade and the consequential effects across trophic levels is that of Yellowstone's wolves. Between the years of 1914-1926 the grey wolf (*Canis lupis*) was actively hunted within Yellowstone National Park after they were considered a threat to the ungulate species found throughout the park. By 1926 it was widely accepted that wolves had been driven from the park, except for a few 'probable' sightings (Weaver, 1978). With the lack of a natural predator, the population of Rocky Mountain Elk (*Cervus Canadensis nelsoni*) began to increase drastically (Ripple and Larsen, 2000). As a result of this the aspen tree (*Populus tremuloides*) suffered greatly from over-browsing by the elk (Smith *et al*., 2003). This decline led to the decision to reintroduce wolves back into the park in 1995-1996, which was followed by a decrease in elk numbers and a restoration of aspen (Ripple and Beschta, 2007). This increase in aspen also led to an increase in bison (*Bison bison*) populations and an increase in willow trees (*Salix* spp.), which were being browsed on by elk in the absence of aspen. This willow increase consequentially resulted in an increase in beaver (*Caster canadensis*) populations within the park, which rely heavily on willow for both food and dam building (Ripple and Beschta, 2011).

These factors and examples demonstrate the importance of carnivore conservation. Carnivores' high vulnerability to extinction, both locally and worldwide, and their importance at the top of the food chain demonstrates how increased efforts are fundamental for the preservation and conservation of biodiversity (Hebblewhite *et al.,* 2011). Of the carnivore species at highest risk, the Siberian tiger (*Panthera tigris tigris*, formally recognised as *Panthera tigris altaica* (Kitchener *et al.,* 2017)) and the Amur leopard (*Panthera pardus orientalis*) are both particularly noticeable. The extreme fragmentation of their habitats, ongoing conflict with humans and the inbreeding complications that come with small populations make the conservation efforts for these two cats enormously important for both their own populations and also the stability of the trophic systems within their Far East Asian ecosystems (Wang *et al*., 2016).

1.1.2 Carnivore Ecology

Despite being some of the world's most revered species, many large carnivores are under increasing threat. Over the previous two centuries substantial population losses have been recorded across many areas (Ceballos and Ehrlich, 2002). This is exemplified across the Mexico-USA border where the grizzly bear (*Ursos arctos*), the wolf (*Canis lupis*) and the jaguar (*Panthera uncia*) have all suffered population decrease, range reduction and regional extirpation, with the wolf and grizzly bear reduced to less than 5% of their former ranges (Grigione *et al*., 2009; Berger *et al*., 2001). A further demonstration of this loss is seen in the cheetah (*Acinonyx jubatus*), which was once widespread across the African continent anpd large parts of Asia. They are now only recorded in 10% of their African range while the Asian population has been largely extirpated with Iran being considered the last stronghold (Farhadinia and Hemami, 2010).

The position of carnivores at the top of the food chain means they are naturally present in smaller numbers than their prey counterparts (Ripple *et al*., 2014). Their large body size results in high metabolic demands, requiring large ranges with a large number of prey. A slow fertility rate and extensive parental care is also prevalent with all carnivores (Ripple *et al*., 2014). The combination of these biological and ecological factors and the increasing conflict with humans is what makes these species exceptionally vulnerable to persecution (Ripple *et al.,* 2014; Wang *et al.,* 2016).

1.2 Threats to Large Carnivores

The biggest and most drastic pressure these species face is that of humans. Throughout the history of human kind there has been a “deeply rooted hostility” for large carnivore species and the negative effects they are thought to have on human lives and livelihoods (Chapron *et al.,* 2014, p. 1517). Conflict between humans and large felids appears to be on the rise (Treves and Karanth, 2003), with predation of livestock and game resulting in retaliations and preventative measures, which often bring about the death of the felids. Evidence for human-felid conflict has been recorded in 75% of felid species (Inskip and Zimmermann, 2009). Within the Russian Far East, conflict between tigers and people is seen where the two coexist. The tigers have been seen taking domestic animals and are often killed in fear or in retaliation. These retaliation killings alone made up 29.5% of recorded tiger mortalities between 1970 and 1990 (Goodrich, 2010).

In many areas poaching and hunting are still huge threats, despite most carnivore species having legal protection (Liberg *et al*., 2012). Numerous species are poached commercially for their fur and pelts and also for use in some traditional medicine (Gratwicke *et al.,* 2008; Kenney *et al.,* 1995). Protected areas offer protection for some populations of species of conservation concern but those outside of these areas remain at extreme risk. The Scandinavian population of Gray wolf has suffered hugely from poaching with simulations suggesting that the population would be four times larger than current numbers had they not been affected. These wolves largely exist in areas where active protection is severely lacking (Liberg *et al*., 2012). The Terai Arc Landscape, across the India-Nepal border, can really exemplify the effectiveness of protected areas. It is extremely fragmented and hence, many of the landscapes large mammals are now confined in protected areas where the presence of consistent anti-poaching teams has been able to apprehend poachers. As a result, his landscape now boasts one of the highest wild Bengal tiger densities in the world Wikramanayake *et al*., 2010).

Of the worlds many ecosystems, few are highly managed or protected. Those that do are currently under increasing threat by the drastically increasing human population and consequential expansion. This brings about fragmentation and habitat loss, which is the greatest threat to the world's carnivores, as well as most other species (Chapron *et al.,* 2014). The increasing human population across South and Central America and the consequential exploitation of natural space has seen a 50% range loss for the jaguar (*Panthera onca*) in the last 100 years (Jędrzejewski *et al*., 2016; Sanderson *et al*., 2002). Formerly a key ecosystem for the jaguar, the Atlantic Forest biome suffered heavily during the second half of the 20th century from deforestation and the conversion of forest areas into livestock ranges and farms. These was effects were visible from satellite images (Haag *et al*., 2010).

1.3 The Importance of Ecological Modelling

1.3.1 Background

The use of modelling techniques in ecology and conservation biology has become fundamental in recent years with these techniques allowing for the geographic distributions of species to be modelled as well as the ability to study spatial patterns and species diversity (Phillips and Dudik, 2008; Graham *et al.,* 2006). The use of computer-based predictive modelling appears to have originated in the early 1970s, with a study by Austin (1971) investigating the environmental determinants for the distribution of inland scribbly gum (*Eucalyptus rossii*). This was followed by a niche-based, spatial crop-species prediction by Nix *et al.* (1977), the earliest species distribution model. Since their first appearance in the literature, the use of predictive models has increased significantly, supported by parallel developments in computer and statistical sciences (Guisan and Thuiller, 2005). Computer designed Geographic Information Systems (GIS) are now becoming common-place in analytical biology. When used in conjunction with a maximum entropy-modelling programme (e.g.

MaxEnt), an approximation of a species' ecological niche, and how it is dependent on the environmental variables chosen, can be projected into geographical space (Phillips *et al.,* 2006).

1.3.2 Ecological Modelling in Carnivore Conservation

This new and evolving science is becoming an incredibly useful aid to big cat conservation. When investigating and predicting the potential distribution of the jaguar (*Panthera onca*) in Mexico, a region where the cat is considered a critical conservation concern, over 300,000 km^2 of suitable habitat was revealed (Rodríguez-Soto *et al.,* 2011). Using bioclimatic variables, alongside other distribution-influencing factors, a model demonstrating the areas that have a high ecological suitability was created. This revealed that more efforts should be focused in these regions with them previously not considered as important as is now believed possible (Rodríguez-Soto *et al.,* 2011).

The cougar, a member of the Felinae subfamily rather than the Pantherinae to which the *Panthera* members belong, historically inhabited most of continental north and South America (O'Neil *et al*., 2014). They were extirpated from Midwestern America in the early 1900's but efforts have been made to model the potential habitat that still exists for cougars in this region of North America (LaRue and Nielsen, 2008). Using land cover, human density, distance to roads, slopes and distance to water as input variables, a model stretching across nine Midwestern states revealed six large areas (>2500 km^2 each) with a habitat suitability greater than 75%, encompassing a total area of 53,700 km^2 (LaRue and Nielsen, 2010).

1.4 Carnivore Reintroduction Programmes and Studies

Reintroduction of locally extirpated carnivore populations to aid in the restoration of the natural integrity of ecosystems is becoming a more and more common tool in conservation and wildlife management. Yet reintroductions present many difficulties, which must be overcome for the programme to be a success (Devineau *et al.,* 2010). There have been many successful reintroductions of predators in the past.

Beginning in 1999, a programme to reintroduce the Canadian lynx (*Lynx canadensis*) to Colorado, part of its historic range, was started. The historic population in Colorado was largely extirpated by the 1980s due to human-induced deaths (Meaney, 2002). From 1999 to 2006, 218 wild-caught lynx from Canada were translocated and released. Since, there has been confirmed sightings of young and hence, successful reproduction within the reintroduced Colorado population (Wild *et al.,* 2006). The areas that were selected as reintroduction sites were chosen with reference to prey availability, the potential for human impacts and available habitat. Although better quality habitat was found elsewhere, it was described as fragmented and so not a suitable reintroduction site. The chance of mortality of the reintroduced population within the habitat must also be considered. The site chosen for the lynx was considered to have the lowest chance of mortality, which proved true as there were significantly less deaths in this area than those outside which the lynx had moved into (Devineau *et al.,* 2011). Although mortality was found to be highest immediately after release, it decreased significantly over the next year. The initial deaths were likely related to stress, with intraspecific competition during exploration and territorial disputes. The study by Devineau *et al* (2010), investigating the mortalities of the reintroduced lynx, found that over time the mortality rates both inside and outside decreased significantly.

The Eastern Cape of South Africa was once home to many of Africa's large carnivores that were driven from the area following conflicts and disturbances by humans. Lions, African wild dogs (*Lycaon pictus*), spotted hyaenas (*Crocuta crocuta*) and cheetah (*Acinonyx jubatus*) were all once common here (Woodroffe, 2000). Reintroductions of these four carnivores have all been attempted in the Eastern Cape after a significant increase in large-scale conservation estates (Hayward *et al*., 2007a). Of them all, the lion has been the most successful, with worries now that overpopulation may become a serious problem. Both the African wild dog and the spotted hyaena have seen population increases as well. With breeding populations now present, the reintroductions of these three species appear successful (Hayward *et al.,* 2007a). The presence of preferred prey and the absence of human conflicts and negative interactions have made the areas selected for reintroduction successful. It must be noted that these reintroductions are in reserves where the borders are fenced. The cheetah reintroduction however, was not successful. The factor associated with this result is the presence of other dominant predators, which may outcompete cheetahs. Other cheetah reintroductions elsewhere, where these other predators are not present, have led to successful programmes (Hayward *et al.,* 2007a).

These previous carnivore reintroductions, with examples of both successful and unsuccessful programmes, demonstrate what is needed for newly-established populations to thrive. A full understanding of each species' respective key drivers will increase the likelihood of a successful programme and hence, the highest chance of survival and the creation of a sustainable populations.

1.5 Ecological Corridors

Both the Siberian tiger and the Amur leopard suffer significantly from habitat fragmentation, with this projected to worsen with increasing human population, potentially leading to an even lower genetic diversity for isolated big cat populations. For this to be prevented ecological corridors are required, these allow easy movement of species between suitable ecosystems (Miquelle *et al.,* 2015). These corridors can increase both local and regional population persistence and are now becoming a common sight in conservation and reserve plans (Rosenberg *et al.,* 1997). The tiger population in India currently has a high gene flow despite much of its habitat being fragmented. Corridors between four of the main tiger habitats have enabled easy movement between them, thus preventing the isolation seen in many of the tiger's other worldwide habitat (Sharma *et al.,* 2013). Wikramanayake *et al* (2004) investigated the potential for corridors for the tiger in the Himalayan foothills, an area that is now highly fragmented. Their analysis discovered, using GIS, that ecological corridors can be restored between all the protected areas and other core habitat in the region. This would link previously isolated populations. Genetic analysis of Siberian tiger populations has already revealed that the sub-population in southwest Primorye and the Sikhote-Alin Mountains are genetically distinguishable, meaning that corridors between all prospective areas will be fundamental to prevent further divergence, if that is the preferred goal (Miquelle *et al*., 2015).

The prospects for corridors for the Siberian tiger and the Amur leopard have already been investigated in a region of the Razdolnaya river basin. A potential corridor between southwest Primorye and the southern region of the Sikhote-Alin mountains was found with much being within forested regions. However, a major highway still poses a problem for the corridor. Miquelle *et al* (2015) suggested the use of overpasses or underpasses to allow for the free movement of both the tiger and the leopard.

These corridors are essential when designing a reintroduction plan for the species as a whole, as the reintroduced populations must be able to move freely between suitable sites as well as those occupied by the original populations. With the Amur leopard being at a huge risk due to isolation, this is particularly important for this big cat and could help to alleviate this current problem.

1.6 Carrying Capacities

When considering reintroduction programmes, knowing and understanding the carrying capacity of the species within the designated site is essential. Overpopulation can have drastic effects on both the introduced predator species and also on the species already present (Hayward *et al.,* 2007b). Although they can vary greatly, carnivore densities within an ecosystem commonly reflect the densities of their prey (Fuller and Sievert, 2001). Previous estimates of carnivore carrying capacities were based on the body weight of prey, with a different range of 'preferred' prey described for each of the carnivores present in the ecosystem (Stander *et al.,* 1997; Laurenson, 1995). However, the biomass of preferred prey species is now the best-recognised method. This method allows for much more successful predictions of carrying capacity, allowing for more accurate population viability analyses. This not only helps to avoid the problems associated with overpopulation but also saves on conservation management costs, allowing a more precise and measurable target for reintroduction projects (Hayward *et al.,* 2007b).

Analysis of the Siberian tiger and Amur leopard habitat in the northern parts of the Changbai Mountains, Northeast China, estimated that the 10,000km^2 area suggested for management would support 30-50 breeding tigers and 50-90 breeding leopards (Wang *et al.,* 2015). This however was estimated from the total area and so the inclusion of prey would give a much more accurate estimate for the area and hence, conservation efforts could be increased and more focused.

1.7 Taxonomy

The taxonomy of the genus *Panthera* has been contested for many years. It is now widely recognised to contain five species; the tiger (*Panthera tigris*), the lion *(Panthera leo*), the leopard (*Panthera pardus*), the jaguar (*Panthera onca*) and the snow leopard (*Panthera uncia*). Each of these also has a number of sub-species. The tiger species, originally described by Linnaeus in 1758, has been historically recorded as having two or more subspecies. Following a recent revision by the Cat Specialist Group (CSG) in 2017 (Kitchener *et al.,* 2017), for instance, the IUCN has now split the previous 6 subspecies and now recognises only two tiger subspecies, 2008). These two subspecies are the mainland tiger (*Panthera tigris tigris*), composing of the Bengal, Malayan, Indochinese, South China and Siberian populations, and the Sunda islands tiger (*Panthera tigris sondaica*), whose only extant population is in Sumatra (Kitchener *et al.,* 2017). The taxonomy of the leopard (*Panthera pardus*) was also part of this *Panthera* revision. Also first described in 1758 by Linnaeus, the leopard was recognised as having nine subspecies (Uphyrkina *et al.,* 2001). The revision by the CSG classifies the leopard now as having eight recognized subspecies, with the North-Chinese population now supposedly subsumed into the Amur leopard subspecies (Kitchener *et al.,* 2017).

With Siberian tigers and Amur leopards being sympatric throughout most of their ranges and currently suffering hugely from population loss, geographic isolation and the resulting consequences, this study will be focusing on these specific populations. The Siberian tiger population, when listed as a distinct subspecies, is formally named *Panthera tigris altaica*, and for the purpose of the study this will be referred to as the Siberian tiger. The study will also only be focusing on the population of Amur leopard in the Russian Far East and surrounding areas. The North-Chinese population, formally known as *Panthera pardus japonensis*, will not be considered. Henceforth, for the purpose of this study, the term Amur leopard will only be referring to the population in the Far East.

1.8 Siberian Tiger Ecology

The largest-bodied and most northern of all tiger populations, the Siberian tiger has a long history with humans and is recognised worldwide. But, if its current population trajectory continues, this captivating predator could face tragic consequences (Miquelle *et al.,* 2012).

1.8.1 Distribution

Before the turn of the 20th century, the Siberian tiger could be found across the Russian Far East, north-eastern China, Eastern Mongolia and throughout the Korean peninsula with a population above 3000 individuals (Dou *et al.,* 2016). Over the next century a number of factors have led to a drastic decrease in this population and its consequential range. The population within the Russian Far East was said to be less than 30 individuals in the 1940s (Miquelle *et al*., 2010). However, it was not till 1969 that the species was first declared endangered (Seidensticker, 2010) and just before the turn of the 21st century that the Siberian tiger was said to be on the brink of extinction (Xiaofeng *et al*., 2009). This led to a number of conservation efforts, which helped the population to avoid this catastrophe (Miquelle *et al.,* 2011). Following this, recent estimations have varied but a 2015 census, set up by WWF Russia (2015) now estimates the population in the Russian Far East as between 480-540 individuals. This Russian population occupies approximately 95% of the existing Siberian tiger range, with the other small group being in north-eastern China (WWF Russia, 2015), however only 3.4% of their range occurs in strictly protected areas (Riley *et al.,* 2017).

1.8.2 Population Loss and Current Threats

The decline of Siberian tigers can, almost entirely, be attributed to anthropogenic disturbance and the ever-increasing human population. The tiger is considered by many to be the most notorious for conflict with humans, with a large mortality count for both species throughout their shared history (Goodrich and Miquelle, 2005). Today, 93% of occupied Siberian tiger range is co-occupied with humans, presenting many potential problems (Goodrich *et al.,* 2010). A key event associated with drastic damage to the population in the Russian Far East was the Russian Civil War (Matthiessen, 2001). Armies based in Vladivostok contributed substantially to the destruction of local populations. In the early to mid-1900s, other tiger populations in north-eastern China became cut off and fragmented following the creation of railroads (Matthiessen, 2001). It wasn't till 1947 that hunting of the tiger became illegal in Russia, but by this point sizable damage had been done. Unfortunately, with the dissolution of the Soviet Union, hunting again became a severe threat (Matthiessen, 2001). Illegal poaching is still a huge problem today. Data collected between 1976 and 2005, investigating mortality, found that 75% of the radio-collared tigers were killed by poachers (Goodrich *et al*., 2008). Along with habitat loss, these present the key problems Siberian tigers face in this region. Range fragmentation and prey depletion, as a consequence of habitat loss, also pose major threats. These are all brought about by increasing anthropogenic land use in areas needed for the extremely large territories required for the tiger (Wang *et al.,* 2016). When considering conservation efforts for the Siberian tiger all of these potential threats must be seriously considered and every effort must be made to prevent them combining to drive the population extinct.

1.9 Amur Leopard Ecology

The Amur leopard is the only leopard subspecies adapted to a cold and snowy climate, making its appearance easily distinguishable from the other usually tropical subspecies (Uphyrkina and O'Brien, 2003). Despite being so unique, this subspecies is widely considered the most rare of all big cats (Hebblewhite *et al.,* 2011) with the IUCN first listing them as critically endangered in 1996 (Uphyrkina *et al.,* 2002).

1.9.1 Distribution

The Amur leopard was once spread throughout the mixed Korean pine-broadleaved forests of northeastern China, the Russian Far East and the Korean peninsula (Jiang *et al*., 2015). It was in the 1990s that the subspecies disappeared from China, with the population in the Russian Far East being reduced to within the south-western region of Primorksy Krai (Wang *et al.,* 2017). The existence of a population in North Korea is unsure. There is little, reliable evidence in the scientific literature suggesting their persistence in North Korea (Uphyrkina and O'Brien, 2003). A population survey in 2012-2014 estimated the world population of the Amur leopard at less than fifty, with the majority of these in the Russian Far East (Wang *et al*., 2016). A population has also moved back into regions of north-eastern China, but these could be as little as 10 individuals (Yang *et al.,* 2016). The most recent survey, a 2018 camera trap census within the Land of the Leopard National Park, now states the park's population alone is over 100 with 84 of these adults (WCCA, 2018). Despite the small rise in numbers, these populations are suffering heavily from severe fragmentation attributed to anthropogenic induced habitat modification (Wang *et al.,* 2017). This has brought suggestions that the population is at a viability threshold with other factors also contributing to the decline of this big cat (Sugimoto *et al.,* 2013).

1.9.2 Population Loss and Current Threats

Like the tiger, the key threats that the Amur leopard faces are anthropogenic influences. The over-exploitation of their prey species by humans throughout Russia, China and the Korean peninsula has led to a reduction in the size of blocks of suitable habitat, bringing individuals into direct competition with each other as well as into areas of higher human disturbances (Wang *et al.,* 2017). This closer proximity to humans also contributed to the increase in poaching of the leopard due to their unique and characteristic coats, which can fetch high prices in many illegal fur markets. Their bones have also been used in traditional medicines (Prynn, 1980). This encroachment further and further into the leopard habitat has also led to a large depletion of prey species as well as causing habitat fragmentation (Yang *et al.,* 2016; Uphyrkina *et al.,* 2002). An increasing trend with farmers in the Russian Far East is the use of fires to clear land for the use of agriculture and the grazing of domestic livestock (Miquelle *et al*., 2004). The fires burn off dead material creating large areas of fertile land thus destroying regions that are habitat for the leopard. In some cases these fires have also spread, destroying much larger regions than originally intended, thus limiting the leopards habitat even further. The repeated fires have given rise to large open grassland habitats, which the local forest ungulate species avoid and consequentially, so do the leopards (Miquelle *et al.,* 2004). Fire is not the only form of habitat loss that the Amur leopard suffers from. With human expansion and population pressures increasing at an incredible rate, the encroachment into the already limited leopard habit is only driving the population down further. Perhaps the largest threat that the remaining Amur leopards face today is inbreeding, which is common with small isolated populations (Uphyrkina *et al*., 2002). This can result in inbreeding depression. With direct contact with wild Amur leopards impossible, due to their conservation needs, genetic studies have not been done, however a decrease in the size of litters has been noted by field studies (Uphyrkina and O'Brien, 2003). Possibly a back-up population could be derived from captive leopards around the world, although this would require extensive genetic history studies to identify suitable individuals for the programme and create the largest gene pool possible. This has now led to studies stating that reintroduction is now the best option if we are to save these leopards from the increasingly likely extinction (Jiang *et al.,* 2015).

1.10 Conservation Efforts

With the current declining population trend of both species expected to continue and the likelihood of extinction becoming more likely, many programmes have been set up aiming to combat this decline. The elusive nature of big cats, Siberian tigers and Amur leopards especially, has made monitoring and distribution studies incredibly difficult. Historically, surveying areas for tracks in various substrate was the method widely used to identify the presence of a species (Silveira *et al*., 2003). However, with Amur leopards and Siberian tigers residing in areas of heavy snow, these surveys could only take place in the presence of fresh snow, with the tracks only lasting for a limited time (Hayward *et al.,* 2002; Hebblewhite *et al.,* 2011). This very much limited the areas which could be surveyed and the time of year they could be completed. The more recent introduction of camera traps and their subsequent development has massively increased the effectiveness of monitoring programmes, especially for species that are so elusive in nature (Carbone *et al*., 2001; Wang *et al*., 2015). As well as being able to survey areas that are not always accessible, they can also continue surveying all year round. One such survey by Wang *et al* (2016) was able to gather occurrence data from 380 camera traps for 175,127 trap days. These cameras also enabled studies to identify individuals more easily by use of coat patterns rather than using tracks alone to attempt to differentiate. This has allowed for more accurate population estimates (Miquelle and Kostyria, 2012). The latest camera trap surveys report the Russian Amur leopard population at 103 (WCCA, 2018).

The use of these methods helped to confirm the worryingly low numbers of both of these big cats and as a result, the Russian government merged three already established parks with a region along the Chinese border to create the Land of the Leopard National Park (LLNP) (Sugimoto *et al*., 2013). This park encompasses approximately 60% of the current range of the entire Amur leopard population, along with all the known breeding grounds, and therefore is fundamental for their conservation. This park was given substantial funding by the Russian government with the aim of protecting the small habitat the leopard still has (WWF, 2012). Specific work on conserving the Siberian tiger has also been amplified since the 2010 St. Petersburg Tiger Summit; all countries where tigers are currently extant attended this. Together they set up the Global Tiger Initiative (GTI), which aimed to double worldwide tiger numbers by 2022 (Wikramanayake *et al.,* 2011).

In conjunction with the LLNP, initiatives and programmes have been set up aiming to combat the decline of both the Amur leopard and the Siberian tiger. The Amur Leopard and Tiger Alliance (ALTA) was set up between Russian and western conservation groups with the purpose of securing the future of both big cats (ALTA, 2017). Working in close cooperation with the local community and governments, the alliance aims to inform and teach local people about the best ways to help (ALTA, 2017). In 2014, the Ministry of Natural Resources and the Environment of the Russian federation released the “Strategy for Conservation of the Amur Leopard in Russia” which aimed to not only conserve the leopard in Russia, but also to strengthen the cooperation with China and protect habitat in both countries (Jiang *et al.,* 2015). Along with other charities and organizations, much work has been conducted on conservation and suggesting the best routes for future plans. It is through these alliances and initiatives that the future of the Siberian tiger and Amur leopard rests its hopes.

1.11 Tiger and Leopard GIS Work

GIS and other modelling techniques have been used in previous and on-going conservation efforts for both the Siberian tiger and the Amur leopard. These studies have significantly aided attempts to prevent the extinction of both species. Using many of the variables considered to be fundamental to each species’ niche, this key technique has enabled unused areas considered to be suitable across each of the predators’ current distributions to be recognised. It is in these highly favourable areas that conservation efforts should be focused, rather than areas where environments are perhaps less favourable.

1.11.1 Siberian Tiger

Hebblewhite *et al* (2014), when attempting to identify, conserve and restore Siberian tiger habitat across the Russian Far East (RFE), used a niche-based habitat model approach. This model included the distributions of some of the tigers' prey, along with human activities and environmental variables. After collecting winter snow tracks, in 2004/2005, of both the tiger and their prey, a model for each individual species, showing the probability of their occurrence within the RFE, was produced. Following this, a single hybrid model was created, combining environmental and prey variables to produce an overall ranking of tiger habitat suitability. Hebblewhite *et al* (2014) then identified the regions with the highest suitability as the areas in which conservation efforts should be focused and habitat degradation and fragmentation should be significantly reduced. Having investigated the relationship between the tiger, its prey and the surrounding environmental factors, the study was able to write a series of action plans suggesting which tiger habitats, associated plant groups and ecosystems require the most protection and are under the most threat.

Following the GTI's plan to double the worldwide tiger population, 20 tiger conservation landscapes (TCL) were identified as areas that offer the best hope for meeting these goals (Wikramanayake *et al*., 2011). One such landscape for Siberian tiger recovery is in China. Hebblewhite *et al* (2012) aimed to identify priority areas within this larger Chinese TCL, with a focus on areas that are both politically and scientifically defensible. Using tiger occurrence data from the RFE and the environmental variables associated with tiger presence, the most suitable habitat in which the tigers reside could be deduced. From this an ensemble habitat model, which averaged an expert-based habitat suitability index, an environmental niche factor analysis and a resource selection function was produced. These encompassed various landscape covariates, including human presence and vegetation and were able to identify the most suitable tiger habitat within the Changbaishan ecosystem, Northeast China, even without Chinese locality points to start from. Alongside this, the connectivity between discovered areas were assessed. This was done using a least-cost path analysis, calibrated against known tiger movement in the RFE. After combining the models, the three best tiger conservation areas were identified with an area over 25,000 km^2. Using habitat-based population estimations, this potential habitat could hold approximately 79 adult Siberian tigers. These findings also allowed for a series of actions to be suggested for specific areas including restoration of prey populations, anti-poaching efforts and reducing encroachment of humans.

1.11.2 Amur Leopard

With the Amur leopard populations being at such a critical low, habitat modelling is becoming a vital tool in the fight against extinction. Reintroductions are being suggested as a potential action to salvage this population, but finding suitable sites can prove difficult, with lots of research and analysis required to find the right locations. Hebblewhite *et al* (2011) investigated the Sikhote-Alin mountains region of the RFE to discover the suitability of the ecosystem for the release of Amur leopards. Using previous occurrence data, along with bioclimatic variables, prey distributions and maps of human presence, they were able to locate 10,648 km^2 of suitable habitat within 8 separate patches. These have the potential to hold approximately 105 adults, which could increase the current worldwide population by up to 4 times. One urgent action now considered to be fundamental for the use of these regions as possible reintroduction sites is the protection of the ungulate prey, which suffer heavily from poaching. Hebblewhite *et al*. (2011) also suggested that further habitat models in the rest of the Amur leopard's historic range could offer potential for a much larger population increase.

The presence of the Amur leopard in China has been uncertain for many years with sightings of only a few individuals. There is now increasing evidence for the presence of the leopard in north-eastern China, with individuals moving across the Russian border. However, the Hunchun-Primorksii Krai region in which the Amur leopard resides has now apparently, far exceeded its carrying capacity (Wang *et al.,* 2016). This uncertainty has led to studies investigating whether there are further areas, within the leopard's historic range, that are suitable habitat today. Using occurrence data from 2004-2014, Jiang *et al* (2015) were able to identify 21,173.7 km^2 of suitable habitat within a region of the Jilin province, along the Russian border. Using four prey species, red deer, roe deer, sika deer and wild boar, as a combined variable displaying the occurrence probability of prey, they stated that it is the presence of prey that drives the leopards' distribution. It is estimated that this area in China has the potential to hold approximately 195 adult individuals.

1.11.3 Next Steps

These previous mapping works on both species have already shown that there are areas within their historic ranges that are still suitable, and which could act as successful reintroduction sites with increased conservation work, along with serious action plans put in place to preserve prey. However, these studies have not included the entirety of each of the big cats' historic ranges and therefore there is still much potential to identify further areas. The inclusion of these new areas will simultaneously investigate further the key factors and variables that can drive the distribution and the population success of each of these incredibly rare cats.

1.12 Three Key Drivers

Following an assessment of the literature exploring the factors that are critical to driving the distribution of predators, I have identified three key drivers. These drivers heavily influence the areas which an individual can spread into and also affect the population size the area can hold. These three drivers are: 1) The presence of appropriate prey 2) Humans and anthropogenic disturbances 3) Interspecific competition.

1.12.1 Presence of Prey

The acquisition of prey is part of the ecology of every predator, therefore any successful conservation program must start from solid knowledge of the diet and prey selection of the target predator. A common cause of predator extirpation is loss of prey therefore, when designing any conservation programme the risk of insufficient food must therefore be assessed and mitigated (Zimmermann *et al.,* 2007). The density of a prey species also has a significant effect on the carrying capacity of predators, as they rely heavily upon them. The reintroduction of the black-footed ferret (*Mustela nigripes*) to many of the American states is a well-known reintroduction success story that emphasises the importance of prey availability. With various reintroduction programmes attempted, it was many years before a successful programme and stable population of ferrets was achieved, through a programme that targeted their key prey species, the prairie dog (*Cynomys* sp.). When investigating the successfulness of programs, defined through the survival of individuals at the reintroduction site versus surrounding areas, a clear, positive relationship between sites with a successful reintroduction and a high total relative biomass of prairie dog was recorded (Jachowski *et al.,* 2011).

1.12.2 Human Disturbances and Conflicts

Many scientists and others now believe and argue that we are currently in the sixth mass extinction event. It is widely accepted that humans are the cause. From a sample of 27,600 vertebrate species, 32% have decreased in population size and range, with it being believed that this will have negative knock-on effects throughout the ecosystem (Ceballos *et al.,* 2017). It is the expansion of humans which has had the biggest effect on large mammal predators (Ripple *et al.,* 2014). The IUCN Reintroduction Specialist Group (RSG) state that reintroduction should only occur in an area where the threat that caused any previous extirpation has been correctly identified and removed or sufficiently reduced (IUCN/SSC, 2013). Therefore, human settlements and areas with high human disturbance should be actively avoided when investigating the area’s best suited for reintroduction of both the Amur leopard and

Siberian tiger. Therefore, any conservation and reintroduction should incorporate human impacts into analysis, alongside environmental and prey factors.

1.12.3 Interspecific Competition

Competition between different species is well understood in ecology, being considered an important factor that influences and controls predator populations. The negative effect competition can have on a predator population has been described in many cases. African wild dog populations in both the Serengeti National Park and Ngorongoro Conservation Area fell after an increase in prey consequentially led to an increase in sympatric spotted hyaena and lion populations which outcompete the wild dog (Caro and Stoner, 2002). A previous reintroduction programme of the cheetah in the Eastern Cape was largely seen as a failure. When introduced into areas where the larger spotted hyaena and lion were present, the Cheetah was outcompeted and so a stable population was not reached. However in two of the reintroduction sites where neither of these two other predators is present, the programme was considered a success (Hayward *et al.,* 2007a; Lindsey *et al.,* 2011).

Competition between tigers and leopards has been also been described in Thailand, Nepal and India (Carter *et al*., 2014). Although the species are largely sympatric in these areas, the leopard is seen to avoid the areas in which tiger presence is high, choosing to remain in areas around the edge of tiger habitats. They were also seen to actively avoid predating pigs, despite them being prevalent in leopard diets elsewhere, as these were the favoured prey of tigers (Carter *et al.,* 2014; Steinmetz *et al.,* 2013; Harihar *et al.,* 2011). Therefore when suggesting the most suitable habitats for reintroduction of both species, the competition between them, and also other carnivores if present, must be considered. The option chosen should allow the best chance for a population to settle and become stable. This may mean reintroducing only one species to an area that could be suitable for either or both.

1.13 Aims and Objectives

This study aims to create a suitability model for both the Siberian tiger and the Amur leopard across their entire historic distribution, which has not been previously done and hence, following on from previous work by those such as Jiang *et al.* (2015) and Hebblewhite *et al,* (2014).

Chapter 2 will investigate the methodology and present the methods required for the creation of this suitability model. This model will aim to use a variety of biotic and abiotic variables all linked to tiger and leopard distribution and their selection of habitats. It will employ maximum entropy to find the areas considered most suitable based on current distribution data and therefore review the importance of each variable upon their distribution. The model will display suitability on a scale of 0-1 with 1 being the highest suitability. Regions and the areas within them will then be identified, being selected upon their size and suitability value. Chapter 2 will also present a prey model, made up of multiple prey species layers that will be manipulated to display a single output, that will display the variety of prey species that are available, this chosen instead of key prey availability which is commonly used in the literature for these two species. This is to determine if there are prey outside of the key prey that have potential to be part of the predator's diet. Furthermore, A human impact model, made up of a human impact index layer and a road map layer, will display human impact on a continuous scale along with road density. This will allow for the avoidance of areas in which human densities or impacts are high, of which previous studies have stated to have a negative effect on Siberian tiger and Amur leopard occurrence. It also allows for roads, which act as barriers, to be identified and avoided. Following this, carrying capacity estimates will be calculated using a synthesis of data from the scientific literature and the known biology of both species.

Chapter 3 will then aim to present the results of the study and further discuss then. These results can then be compared with other studies that have been done previously to attempt to understand differences and similarities. This, with the aim of, helping to understand the requirements and variables of Siberian tiger and Amur leopard occurrence. As part of this, using these three models, areas and regions can be selected as being suitable for future Siberian tiger and Amur leopard populations. These regions can then be critically analysed, investigating their size, distance from the current populations and its importance to its respective species. Competition between the leopard and tiger will then be considered with shared suggested regions being prioritized to a particular species. These regions will then be given the conservation priority title whilst also presenting the carrying capacity estimate and hence the number of individuals that these new areas could possibly support.

The final chapter aims to discuss and investigate the findings of this paper in terms of its broader conservation impacts. This means the future conservation actions that would be required for a successful population to be established can be discussed. This will take into account current and previous suggestions of conservation plans for both these species and other endangered species and, where possible, use or adapt these to best aid each of these two species. This chapter will also aim to include certain conservation actions and ecological corridors, that are a necessity for any future reintroduction. These will be developed through a synthesis of data. The resulting suggestions will then be evaluated with various reintroduction criteria, where their viability can be determined. Finally, a series of action plans will be constructed. These will be suggestions for future work on Siberian tiger and Amur leopard conservation work. They will include suggestions for what should happen if the regions identified in this study are to have promise as future reintroduction areas. These will consider corridors over roads, preventing human disturbances, future monitoring programmes and installation of new nature reserves/national parks. In all, this chapter will present a practical look at how the results of the previous 3 chapters could be possible and what it would require for this.

Chapter Two: Methods and Materials

2.1 Introduction

To achieve the previously mentioned aims and objectives (Section 1.12), this study will employ three different modelling techniques each of which addresses one of the three drivers identified beforehand (see section 1.9). For these models to be achievable, accurate species distribution data is required for both the Amur leopard and the Siberian tiger (see section 2.2 and 2.2 respectively). To produce the basis of each model, environmental variables (see section 3.0), including climatic variables (section 3.1), topographical features (sections 3.2) and vegetation components (section 3.3) are required to build an abiotic suitability model of the target area(s). Prey species and distributions (section 4.0) and human densities and impact (section 5.0) are used for their respective driver model, so their effects can be explored separately. These models will then be combined for each taxon of interest (Amur leopard and Siberian tiger), to produce a single over-arching integrative model that can be used to suggest areas of possible future release and identify regions of especially high or low suitability. This chapter will begin by presenting the data that has been chosen for use as part of the models, explaining their reason for inclusion and source origin. It will then move into a more detailed methods section, explaining how each model was computed and its data processed which will finalise in a suitability model for each of the Siberian tiger and Amur leopard.

2.2 Distribution Data

2.2.1 Amur Leopard

Occurrence data for the Amur leopard was gathered from four separate surveys (Table 1). These were all conducted within the known, current distribution of the leopard. Areas and regions in which the probability of Amur leopards is expected to be very low or non-existent were avoided by the authors. Routes or locations where with evidence of leopards were surveyed using the methods mentioned below (Table 1). All data points collected by these studies fall within the range defined by the IUCN Cat Specialist Group (Fig. 1).

Table 1. *Occurrence data for the Amur leopard collected from literature sources, with the number of data points, the type of data collected and citation.*

Data Collection Period	No. of Data Points	Citation	Occurrence Type
1997-2008 After new snowfall	467	Hebblewhite *et al*., 2011	Snow tracks
2000-2008 During seven winters (Excluding 2003-2004)	239	Sugimoto *et al*., 2013	Faeces, hair and saliva
2004	307	Jiang *et al*., 2015	Photos, killings, tracks and faeces
2015	170	Vitkalova and Shevtsova, 2016	Camera traps
Total	1,183		

2.2.2 Siberian Tiger Distribution Data

Siberian tiger occurrence data was collected from six studies and combined (Table 2). The data collection for these studies all occurred within the current range of the Siberian tiger, as described by the IUCN Cat Specialist Group (Fig. 2). A variety of monitoring techniques were used in distinct studies (Table 2) all of which provided evidence for presence of Siberian tigers. The data sources represent both the populations in the Russian Far East and in north-eastern China. The sampling data (tracks and faeces) from the Russian Far East were all collected from areas or reserves in which tiger presence was known. Those in China helped provide evidence for that population and aided the increasing conservation efforts.

Table 2. *Occurrence data for the Siberian tiger including the number of data points, the method of data collection and the citation. *Two models were created in this study, both were used. **Data from this study is a combination of two previous large scale studies, Sun et al. (1999) and Li et al. (2001). ***Data originates from a study by Matyushkin et al. (1996)*

Data Collection Period	**No. of Data Points**	**Citation**	**Occurrence Type**
2000-2003	81	Goodrich and Miquelle, 2005	Radio Collars and kills
1992-1997(a) 2004-2006(b)	56	Goodrich *et al*., 2010*	Radio Collars
2008-2009	284	Rozhnov *et al*., 2011	Radio Collars
1998 and 1999	784	Xiaofeng *et al*., 2011**	Tracks
1995-1996	113	Tian *et al*., 2014***	Tracks
2009-2010 and 5 days during 2011	6	Caragiulo *et al*., 2015	Faeces
2013-2015	53	Dou *et al*., 2016	Faeces
Winter 2004-2005	1301	Hebblewhite *et al*., 2014	Tracks
Total	2,678		

Figure 1. *The range of the Amur leopard within the Russian Far East and north-eastern China. The yellow represents the extant range while the purple represents the area in which the leopard is 'possibly extant'* Data downloaded from the IUCN Red List (Stein et al., 2016) andedited to only show the Amur population using ArcGIS 10.5.1.*

**Strong evidence now exists for species persistence in the area previously considered 'possibly extant', meaning that this is also part of the current range of the species (Jiang et al., 2015)*

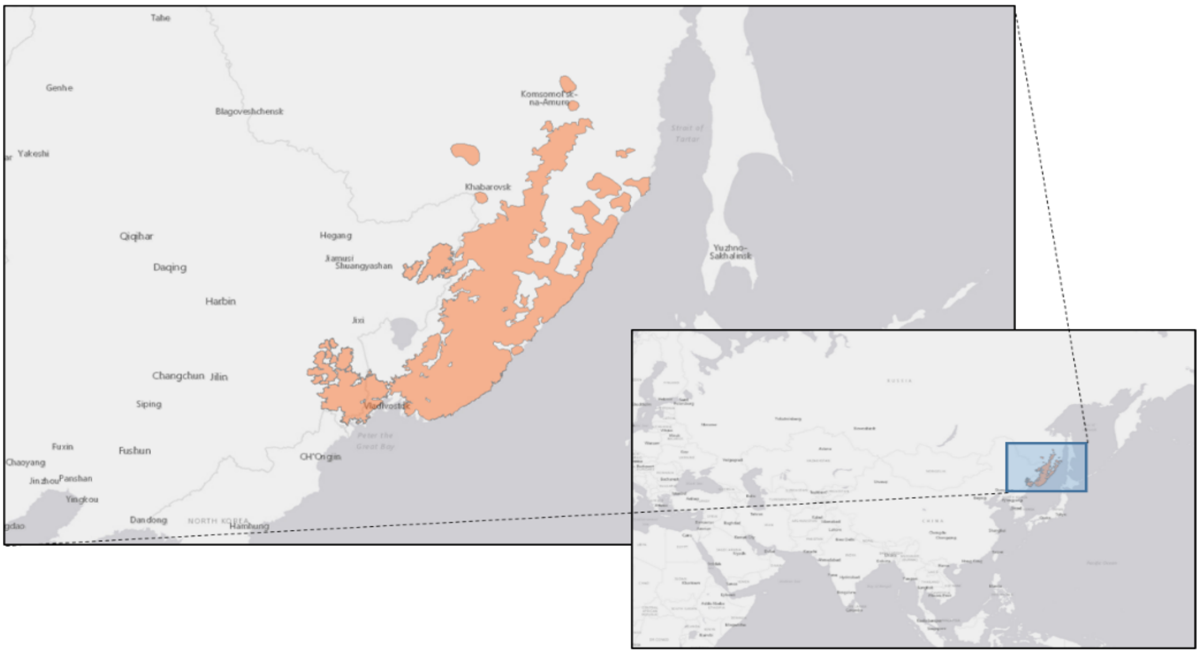

Figure 2*. The current, known distribution (in orange) of the Siberian tiger within the Russian Far East and north-eastern China. Data downloaded from the IUCN Red List (Goodrich et al., 2016). Edited and displayed to only show the Amur population using ArcGIS 10.5.1.*

2.3 Environmental Covariates

*Table 3. The variables selected and used in the three models created for the study. Showing the name of the variable, whether it is continuous or categorical, the categorical category (if applicable), the resolution and the source of the data. * Slope and slope aspect were created from the original digital elevation model using the 'slope' and 'slope aspect' tools respectively from the spatial analyst toolbox in ArcGIS 10.5.1. **The resolution for Terrestrial Ecoregions of the World and IUCN Red List data could not be found. Both these data packs draw upon multiple sources, in multiple sources with different original resolutions. Both these sources are widely used and accepted sources. After running all datasets through the Maximum Entropy modelling, the resulting model has a resolution of 30 arc seconds which therefore means that the resolution of both the unknown sources will be lower.*

Variable Type	Model Used in	Variable Name	Continuous or Categorical	Categorical category	Resolution	Source
Environmental variables	SDM	Annual mean temperature	Continuous	n/a	Approx. 30 seconds (Approximately 1 km²)	WorldClim 2.0 database (Fick and Hijmans, 2017)
	SDM	Temperature seasonality	Continuous	n/a		
	SDM	Annual precipitation	Continuous	n/a		
	SDM	Precipitation seasonality	Continuous	n/a		
Topography	SDM	Altitude	Continuous	n/a	30 metre	Digital elevation model (DEM) SRTM v2 (Farr *et al.,* 2007)
	SDM	Slope*	Continuous	n/a		
	SDM	Slope Aspect*	Categorical	N, NE, E, SE, S, SW, W, NW		
Vegetation	SDM	Biome	Categorical	14 different biome types including forests, grasslands, deserts etc)	n/a**	Terrestrial Ecoregions of the World (Olson *et al.,* 2001)
Prey	Prey Model	Eastern Roe Deer	Categorical	Presence or absence	n/a**	IUCN Red List databank (2018)
	Prey Model	Sika Deer	Categorical	Presence or absence	n/a**	
	Prey Model	Musk Deer	Categorical	Presence or absence	n/a**	
	Prey Model	Wapiti	Categorical	Presence or absence	n/a**	
	Prey Model	Wild Boar	Categorical	Presence or absence	n/a**	
	Prey Model	Moose	Categorical	Presence or absence	n/a**	
	Prey Model	Raccoon Dog	Categorical	Presence or absence	n/a**	
	Prey Model	Asian Badger	Categorical	Presence or absence	n/a**	
	Prey Model	Mountain Hare	Categorical	Presence or absence	n/a**	
	Prey Model	Manchurian Hare	Categorical	Presence or absence	n/a**	
	Prey Model	Red Fox	Categorical	Presence or absence	n/a**	
	Prey Model	Eurasian Otter	Categorical	Presence or absence	n/a**	
Human Disturbance	SDM & Human Disturbance	Human Impact Index	Continuous	n/a	Approx. 30 seconds (Approximately 1 km²)	The Global Human Influence Index (Geographic) V2 (1995-2004) (WCS, 2015)
	Human Disturbance	Asia Roads	Categorical	Road or no road	+/-50m	(CIESEN, 2013)

2.3.1 Climate

To help understand the makeup of the current habitats of both the Siberian tiger and the Amur leopard, a number of abiotic variables were selected for investigation (Table 3). To best give an accurate representation of the climatic requirements for the respective habitats for both species, annual mean temperature, temperature seasonality, temperature annual range, annual precipitation and precipitation seasonality were selected from the WorldClim database. Despite large carnivores displaying considerable behavioural plasticity (Biswas and Sankar, 2001), these abiotic variables still affect their distribution and habitat selection.

Rainfall levels, for instance, are known to determine the growth of vegetation which not only serves as food for the prey of both big cat species, but also offers cover which is fundamental for large carnivores for protection from intense thermal levels, reproduction, stalking prey and escape from unfavourable situations (Trinkel, 2013; Gavashelishvili and Lukarevskiy, 2008). The amount of snowfall can also affect both species. One key limiting factor for the distribution of the Amur leopard is deep snow, as it prefers habitats where the average snow cover is 10-15cm (Miquelle *et al*., 2010). Siberian tigers will also seek refuge from deep snow, which can act as a restraint upon movement, affecting both travel and hunting (Miquelle *et al*., 1999). With global temperatures increasing and snow depth decreasing, this could open new regions that once were considered unfavourable to these species as they become more suitable. The temperature of an area has also been seen as a key distribution factor, with the leopards choosing warmer regions for their home ranges, this being linked to less snow cover (Miquelle *et al*., 2010). The seasonality of temperature and precipitation give the variation of each respective variable and so represent the seasonality of the habitat, which can in turn affect both prey availability and access to territories. Although much debate exists, there is thus evidence suggesting that at least the northern limits of carnivores are determined by abiotic factors, including temperature and other climatic variables (Ferguson and McLoughlin, 2000).

2.3.2 Topography

Within the mountainous regions of the Russian Far East and north-eastern China, a substantial difference in elevation can be found, along with steep slopes and varying slope aspects (Table 3). These are all topographical features that have been found to have an effect on the tigers and leopards' habitat choice and also limit their distribution (Carroll and Miquelle, 2006; Qi *et al.,* 2015).

For the Siberian tiger, both the degree of slope and the elevation are considered key variables for the selection of a home range, with steep slopes actively avoided (Miquelle *et al*., 1999). The presence of the Siberian tiger also correlates with lower altitude, riverine valley bottoms. These are considered easier for travel while also being the chosen topographical habitat of their favoured prey species (Carroll and Miquelle, 2006). The Amur leopard also prefers lower altitude regions, with elevation being considered one of the ecological thresholds for the species (Qi *et al*., 2015). Consistent findings by Qi *et al* (2015) and Hebblewhite *et al* (2011) state that mid-elevation habitats are of the highest quality for leopards, with this being linked to prey availability and also poacher avoidance. Unlike the tiger, the leopard actively searches out slopes with low hill shade values (southerly aspects), which is linked to less snow cover (Hebblewhite *et al*., 2011).

2.3.3 Vegetation

The importance of habitat, and therefore vegetation, on carnivore distribution and habitat selection is often debated. The selection of habitat may be purely based on the highest density of prey, or otherwise on finding areas with lower densities of prey but with cover for hunting, meaning the prey is easier to catch (Balme *et al*., 2006). Vegetation has been found to affect the habitat selection choices of many carnivore species including lions in the Serengeti (Hopcraft *et al.,* 2005), grey wolves in North America (Hebblewhite *et al.,* 2005) and the Puma, another large stalking predator much like the tiger and leopard (Spong, 2002).

As stalking predators, both the Siberian tiger and the Amur leopard rely upon cover to get close to prey before killing, unlike other predators which will chase down prey (Karanth and Sunquist, 2000). Leopards in Africa have not been recorded hunting in short grasslands where there is no cover (Hayward *et al*., 2006). Both tigers and leopards have a long-standing association with the Korean pine forests found in north-eastern China and the Russian Far East, with presence of each cat positively related to the presence of this biome (Jiang *et al*., 2015). However, these mixed-broadleaved Korean pine forests have declined substantially (Chen *et al*., 2003), this being suggested as the reason Miquelle *et al*. (1999) found that Siberian tiger distribution was poorly related to these forests. Instead oak forest may be important to the tigers, despite them not always being selected, as they are a more widespread ecosystem option. Distribution analysis in north-eastern China found that the tiger avoided coniferous forests while selecting for deciduous forests alongside the Korean pine (Hebblewhite *et al*., 2012). Jiang *et al*. (2015) also found a strong, positive correlation between Amur leopard density and Korean pine and deciduous forest proportions. Despite the debate about the exact importance that the habitat has for the distribution and habitat selection of both predators, it is widely regarded as at least having a small effect and therefore is included (Table 3).

2.4 Prey

2.4.1 Introduction

With any large predator reintroduction and conservation plans, prey abundance and availability are factors which must be assessed before any action is put in place (Zimmermann *et al*., 2007). The distribution of the Siberian tiger and the Amur leopard are determined by their prey, with the highest densities coinciding with regions with high prey densities (Wang *et al*., 2017; Miquelle *et al*., 1996). Despite predators having preferred prey, which they are evolved to optimally hunt, "prey switching" will occur when these preferred prey are at low densities (Clements *et al*., 2014). The red fox, for example, has been seen to switch between fauns and microtine voles depending on their availability (Kjellander and Nordström, 2003).

Alongside favoured prey, other smaller prey can be just as important for a stable population of carnivores. Smaller prey are taken by old and sick individuals or during the harsh winters of the Russian Far East where prey can be scarce (Goodrich *et al*., 2011). Smaller prey can also be brought back by mothers for their young to kill, with this teaching them the skills they will later require (Caro and Hauser, 1992). These small prey species can often be under considered in dietary analysis of predators as their smaller body sizes can be easily missed, or the whole body can often be digested, unlike with larger ungulates, so their importance can often be under appreciated (Miller *et al*., 2013).

With both the Siberian tiger and Amur leopard only occurring in a fraction of their former ranges, there is potential for novel prey species becoming more prevalent in the diets, through prey switching. Incorporating the preferred prey weights of each predator into assessments of their options can identify possible alternative prey species whose presence may not previously have been considered.

2.4.2 Livestock

Predation of livestock by large carnivores is seen in most areas where both occur. Unsurprisingly the highest rates of livestock predation occur in areas where both livestock and predators are at high densities (Bagchi and Mishra, 2006). When the two coincide, predators will often take livestock that are grazed within or near forested regions, within their habitats (Wang and Macdonald, 2006). However, despite their usually high availability, large carnivores will mostly prey upon wild prey rather than domestic livestock (Kumaraguru *et al*., 2011). For both the Amur leopard and the Siberian tiger, livestock predation mostly occurs when their respective, preferred prey species are at low densities (Soh, *et al*., 2014). In north-eastern China, cattle represented the smallest biomass proportion among all prey consumed by the Siberian tiger and the Amur leopard, this being relatively more than in the Russian Far East where cattle farming is much less. Supporting previous conclusions, the occurrence of the cattle was thought to be due to the possible low availability of preferential prey in winters, with no cattle appearing in the summer diet of the tiger (Yang *et al*., 2018).

Despite them appearing sometimes within the diets of both species (Wang *et al*., 2017), livestock (Including domestic dogs) will not be considered as viable prey for either species for the purpose of this study. This is because livestock predation often brings about retaliation killings along with a link between livestock and poaching (Soh *et al*., 2014). Therefore, when considering the best areas for tigers and leopards, areas *without* livestock are considered better than those with, where attendant risks to carnivores are higher. Jiang *et al*. (2015) stated that conservation should focus on optimising the assembly of prey available, so that switching to livestock is not required. Methods to further limit livestock predation will be discussed further in the project's discussion.

2.4.3 Amur Leopard Prey Preferences

A variety of prey species have been recorded for the Amur leopard across its limited range. The abundance of each species and the primary representatives in leopard diets vary depending on the location of the analysis as well as the season (Miquelle *et al*., 2010). Leopards will prey upon species of a similar weight to themselves or slightly higher, but with a preference for small to medium sized ungulates (Hayward *et al*., 2006; Hebblewhite *et al*., 2011). The roe deer (*Capreolus pygargus*) is seen as the primary prey across the leopard's distribution, with an annual proportion occurrence of 37.5% in north-eastern China (Yang *et al*., 2018). Wang *et al*. (2017) found that roe deer were photographed at 90% of Amur leopard sighting stations, making a clear link between the presences of the leopard and the deer. In Southwest Primorye the sika deer (*Cervus nippon*), which has now become the dominant ungulate, is considered the primary prey source. The relative contributions of the roe and sika deer changes in relation to their relative presence (Miquelle *et al*., 2010).

As previously stated, prey switching, or a smaller change indietary components can often happen where favoured prey are at lower densities, or the presence of a larger carnivore outcompetes the focal taxon (Jiang *et al*., 2015). Therefore, other (non-preferred) prey sources should be considered as just an important and influential in the overall distribution of a predator. The Siberian musk deer (*Moschus* *moschiferus*), another ungulate present within both the current and historical distribution of the leopard, is smaller than the roe deer in stature and has appeared in the diet of the leopard (Jiang *et al*., 2015). Despite its large size, the wild boar (*Sus scrofa*) has been documented in the diet too (Wang *et al*., 2076; Miquelle *et al*., 2010). It is the young that are predominately preyed upon, but not in as high numbers as the deer species (Hebblewhite *et al*., 2011). The Manchurian wapiti[1] (*Cervus canadensis xanthopygus*) is considered much too large to be preyed upon by the leopard and hence does not appear in the very limited dietary analyses of the predator to date. However, the biology of the wapiti could suggest that the young are a possible prey source. During the first few months of life, like many other deer species, young wapiti hide within long grass while their mothers feed. Being born at around 10kg and growing significantly in the first few months (Johnson *et al*., 1951; Wilson and Mittermeier, 2011). With carnivores often selecting young prey (Garrott *et al*., 2007), during this stage the fawns could act as a prey source for leopards, especially when other prey are at lower densities. Although only appearing in small quantities, many small mammals also appear in the diet of the Amur leopard. The mountain hare (*Lepus timidus*), Manchurian hare (*Lepus mandschuricus*), Asian badger (*Meles leucurus*) and raccoon dog (*Nyctereutes procyonoides*) are all such small mammals that appear, to different extents, within the Amur leopard's diet (Miquelle *et al*., 2010; Wang *et al*., 2017). The growing studies and knowledge of the small population within north-eastern China has shown the Eurasian otter (*Lutra lutra*) and the red fox (*Vuples vulpes*) are also preyed upon here (Yang *et al*., 2018). Each of these prey species can be considered a subsidiary component of the Amur leopard's diet. The long-tailed goral (*Naemorhedus caudatus*), is present within the distribution of the Amur leopard however, despite being a similar size to other common prey species, the species is currently under threat with conservation projects ongoing (Zaumyslova and Bondarchuk, 2015) so therefore will not be included as a current prey variable (on the same grounds as livestock were excluded), but if successful conservation efforts

[1] The common name for the wapiti varies with different regions and countries. Elk is commonly used in Europe but is also used as a common name for the moose. Therefore for this study *Cervus canadensis* will be referred to as wapiti and *Alces alces* referred to as moose.

persist and the population increases, the long tailed goral could again become a key component of the Amur leopard's diet.

All the prey species described above save the goral and livestock will be included in this study and they have been split into key and subsidiary prey. Key prey is defined as any species falling within the weight range suggested by Clements *et al*. (2014) for the African leopard. This has been used as a proxy as a weight range analysis for Amur leopard prey does not currently exist. This weight range extends from 10kg up to 45 kg. Therefore, the roe deer and sika deer are here considered the key prey for Amur leopards, with them being the species at the upper end of the range. This is due to roe and sika appearing multiple times in analyses. The other prey species are all to be considered subsidiary to reflect their less certain usage and the fact that they are probably not required for leopard survival if the key prey is present and abundant.

2.4.4 Siberian Tiger Prey Preferences

An extensive body of knowledge currently exists for the Siberian tiger. The fragmented nature of the tiger's current distribution means that different prey sources become more or less influential depending on their density and distribution (Miquelle *et al*., 1996). Like other solitary predators, the tigers preferred prey body mass if approximately equal to their own (Hayward *et al*., 2012). Despite individual tigers showing large variation in the makeup of their diet, the tiger's distribution appears to be complexly linked to the presence of ungulates (Miquelle *et al*., 1996). The primary prey sources of the Siberian tiger are Manchurian wapiti and wild boar, representing a combined 83.8% of the diet within the Sikhote-Alin state Zapovednik Primorye Province (Miquelle *et al*., 1996). Tigers take wapiti of all ages with no significant difference between predation on young and adults, and boar appearing to have similar patterns (Miquelle *et al*., 1996).

In the southern region of the Siberian tiger's current distribution, sika deer have replaced the wapiti as the most abundant cervid. This is represented in the tiger diet, with sika becoming more prevalent in the southern regions (Miquelle *et al*., 2010). Despite being half the size of the Manchurian wapiti and possibly decreasing the tiger's foraging efficiency, populations of Siberian tiger in these sika abundant regions are strong and reproducing effectively (Miquelle *et al*., 2007). This suggests that in regions of the tiger's historic distribution where either the wild boar or Manchurian wapiti are limited, other ungulate species can become a more important (and sufficient) source of food.

Musk deer and badger have also appeared in dietary analysis of Siberian tigers (Miquelle *et al*., 2010). Although only representing a small percentage of the total diet, Asian badgers appear in the diet during the summer months, as they are in hibernation during the winter (Miquelle *et al*., 2009; Miquelle *et al*., 1996). The badger is also considered an important prey source for elderly and sick tigers as they are easily captured (Goodrich *et al*., 2011). They may be taken opportunistically rather than actively hunted (Miller *et al*., 2013). The musk deer also regularly appears in dietary analysis, despite not being preferred due to their smaller size (Hayward *et al*., 2012; Miquelle *et al*., 2010). Moose (*Alces alces*) are also taken opportunistically (Miller *et al*., 2013), but in some regions appear in the diet in larger percentages (Miquelle *et al*., 1996, data from Kaplanov, 1948). Due to the size of moose, it is likely that the representatives in these analyses are young, elderly or sick. Both the musk deer and the moose could therefore still represent an important tiger food source when other prey sources are at low densities.

The division of these prey species into key and subsidiary was determined by whether or not they fall within the tiger's preferential prey weight range, as suggested by Hayward *et al*. (2012), of between 60 and 250kg. This identifies the wild boar, Manchurian wapiti and sika deer as key prey. Both the boar and wapiti appear extensively in Siberian tiger diet studies while the sika appears more prominently in the southern stretches of the tiger's distribution. All other tiger prey mentioned are to be considered subsidiary.

2.4.5 Source Download

Current ranges for the all key and subsidiary prey species were collected from the IUCN Red List databank (2018). These give the global extent of each species, rather than their distributions a local level. This was selected to give a general understanding of the variety of prey species that are expected to be found within the study areas, rather than their localized movement between specialist habitats. The limitations of using this data and the effect is has on the model will be discussed in section 3.3.

2.5 Human Disturbances

The drastic decrease in both of these species' populations is largely attributed to human expansion and poaching. Methods to overcome poaching are heavily debated, with many put into practice with varying levels of success (Galster *et al*., 2010). Until poaching is eliminated and no longer a threat that the Siberian tiger and Amur leopards have to face, every effort must be made to limit these effects. A clear link between poaching, and the associated cub mortality, and roads can be found (Kerley *et al*., 2002). Both small and primary roads serve as transport means for poachers who are able to track individuals, with the roadsides serving as a place they can stop and begin their tracking (Goodrich *et al*., 2008). It is those individual big cats who have territories without roads crossing them that have the lowest mortality rate and, consequentially, the highest reproductive success (Kerley *et al*., 2002), demonstrating the requirements for stable populations to be built and managed. Collisions on roads also represents a significant danger to both species. Within the Sikhote-Alin mountain range of the Russian Far East, analysis of the cause of death of 53 Siberian tigers found that humans caused 72%. 8% of the recorded deaths were caused by vehicles (Goodrich *et al.,* 2008). Mortalities caused by road collisions can actually be seen in many carnivores (Kerley *et al*., 2002). Although many species, like the grey wolf (*Canis lupis*), will actively avoid roads and shift territories to evade them, both tigers and leopards will use roads to navigate throughout their territories as they serve as low energy movement pathways compared with other habitats (Carter *et al*., 2015; Kerley *et al*., 2002). This increasing their risk of collisions and poaching.

While also being at a higher risk of poaching, being within close proximity of human settlements poses further threats to both big cats (Ngoprasert *et al*., 2007). Farms and livestock are associated with settlements, increasing the risk of tiger and leopard mortalities either as retaliation killings or out of fear (Jędrzejewski *et al*., 2017). Within the Congo, leopard densities increase with distance from settlements

(Henschel, 2009), with similar findings for the leopard in Thailand and Gabon (Carter *et al*., 2015). A suggestion to limit these human disturbance effects, which is critical for successful conservation efforts, is zoning. Separating humans and large carnivores and preventing the conflict that often comes about when both are put together is key to this approach (Goodrich, 2010).

To attempt to map, model and prevent these conflicts, the Global Human Influence Index (Geographic), V2 (1995-2004), produced by the World Conservation Society (WCS) and Columbia University Center for International Earth Science Information Network (CIESEN), was selected and downloaded (WCS, 2015). This index combines information on human population density, built up areas, night-time lights, land use, human used coastlines, roads, railroads and navigable rivers. This was selected as giving the best indication of the level of anthropogenic disturbances. The data for Asia was downloaded, displayed at 30 arc-second grid cell (1km grid cells) resolution. Road data produced by the CIESEN was also selected for inclusion in my models, as it displays all major roads across the target area (CIESEN, 2013).

2.6 Data Processing

2.6.1 Occurrence Data

Two ArcGIS 10.5.1 projects were opened, one each for the Amur leopard and Siberian tiger, and a common geodatabase was created with the occurrence datasets imported and then opened within their respective project. Using the 'Georeferencing' tool, each dataset was aligned to its study area and using the 'Create new features' tool, a feature class containing point data was made for each occurrence dataset. This allows more effective quality-control and editing in ArcMap than working with the original .csv or .xls files.

With 3 of the 4 Amur leopard datasets collected within the Land of the Leopard National Park (LLNP), this data was filtered with the aim of eliminating potential bias arising from over-sampling of individual home ranges. This was done per De Angelo *et al*. (2011), with a grid of 5.74 x 5.74 km (the square root of the suggested smallest range of a female Amur leopard, 33 km^2 according to Wilson and Mittermeier (2009a)). Within each grid cell, a single point was randomly selected using the 'subset data' tool with a seed of 0. The dataset from Jiang *et al*. (2015) in north-eastern China represents the only data used from this area and therefore point data did not intersect other samples as the combined LLNP data did; this step was not needed here.

The Siberian tiger data was filtered in its entirety. Again, following the methods put forward by De Angelo *et al*. (2011), a 14.14 x 14.14 km grid was placed across all points, as 200 km^2 has been suggested by Wilson and Mittermeier (2009b) as a minimum female territory size. A single point was selected from within each grid cell using the same procedure. The two-occurrence datasets were then exported to .csv files for use in subsequent modelling.

2.6.2 Environmental Covariates and Human Impact

Eight environmental variables were selected as potentially influential for both Siberian tiger and Amur leopard distributions. Environmental variables, relating to topography, climate, vegetation, alongside human disturbances were considered. The general framework of which can be seen in Fig. 3. Altitude data was extracted from a digital elevation model (DEM), to cover an area greater than the historic distribution of both the Amur leopard and the Siberian tiger. All tiles were uploaded to the common geodatabase and using the 'mosaic to new raster' tool were combined into a single raster layer. From this single elevation map, slope was calculated using the 'slope' tool (spatial analyst toolbox). The direction, or aspect, of the slope could also be calculated using the 'slope aspect' tool, which produces a map of slope orientation in degrees which can then be categorized into N, NE, E etc. These three topographical variable maps were then saved to the common geodatabase. The Terrestrial Ecoregions of the World (TEOW) digital map was also uploaded to the common geodatabase, with the mutually exclusive biome classes selected and then converted to raster format using the 'polygon to raster' tool. Global maps of the four climatic variables selected from the WorldClim database were obtained and saved to the common geodatabase for manipulation. To account for the anthropogenic disturbances, the Human Influence Index (HII) was also uploaded and displayed on a continuous scale.

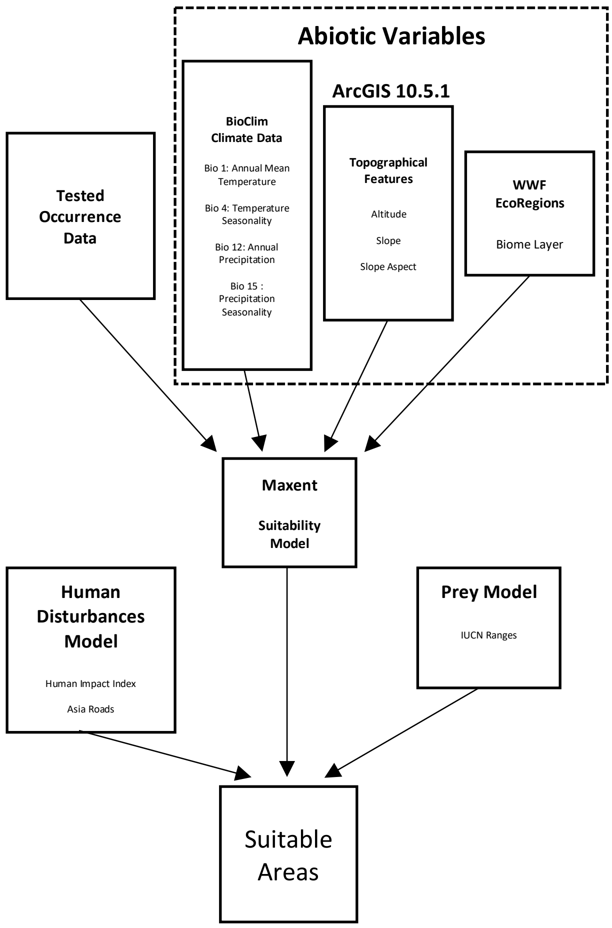

Figure 3. A general framework for the study. Variables and occurrence data were uploaded to ArcGIS 10.5.1 within the layers then being used in Maxent to give a maximum entropy suitability model. This was then analysed alongside the human disturbances and prey models to suggest suitable areas.

Each of these environmental covariate and human disturbance layers were trimmed to the default extent using the ‘clip’ tool and also to a default cell size and resolution (0.008333˙) or 1-arc second ($1km^2$) using the ‘resample’ tool. This 1-arc second resolution comes from it being the lowest resolution of all inputted variables and therefore all others are converted to this. The eight environmental layers and the HII, with default extent and cell size, were converted and saved as .ascii files to a common folder.

2.6.3 Modelling in MaxEnt

For the creation of the two Species Distribution Models (SDM) models, I chose MaxEnt v.3.4.1(Phillips *et al.,* 2019). This particular modelling technique achieves high predictive accuracy and allows for a probability distribution value over the study area using known presence locations. Maxent is also a method that considers presence-only data and with the range of both species unknown in many regions, predicting areas of absence would be unsuitable. This method has also had significant prior use across modelling studies and appears to perform better than other methods (Jorge *et al.,* 2013). When identifying potential areas, the mean of each variable must be close to the recognised mean seen across the sites of known presence (Phillips and Dudík, 2008).

The model was conducted with 5000 maximum iterations and 10000 background points plus presence points for each of the Amur leopard and Siberian tiger (10,147 for the leopard and 10,457 for the tiger). 75% of the data was used for training and 25% for testing. which Jackknifing was used to analyse variable importance, enabling the estimation of bias and standard error (Kebede *et al.,* 2014), and response curves were also created to allow exploration of the cats' responses to each individual environmental variable. The logistic output format was selected, as suggested by De Barros *et al.* (2012). This gives each grid cell a continuous value from 0 (least suitable) to 1 (most suitable), with these expressing the probability of the area being of suitable environmental conditions (Jorge *et al.,* 2013). To be able to differentiate between areas of suitability and unsuitability the threshold value 'maximum test sensitivity plus specificity' was applied to outputs. This demonstrates the probability that the model correctly predicts the observation of a species at a specific site (sensitivity) and the probability that an absence is correctly predicted at a given site (specificity) (Liu *et al.,* 2011). Excluding sites that fall below this threshold reduces the risk of selecting sites considered unsuitable (De Barros *et al.,* 2012).

The performance of individual models can be evaluated using the area under the curve (AUC), used as a measure of the model's overall performance, demonstrating the probability that a randomly chosen occurrence site is selected over a randomly selected site (Kebede *et al.,* 2014). The AUC will be <1 as random points (in IUCN locations not present in the occurrence dataset) were used alongside known locations. An AUC of 0.5 will indicate that the model predicts areas no better than chance, so AUC values close to but not identical to 1 (which indicates perfection or overfitting) are preferred (Kebede *et al.,* 2014).

2.6.4 The Amur Leopard MaxEnt Model

Amur leopard occurrence data for the LLNP, and surrounding areas of the RFE, and north eastern China were separated, saved as separate layers and converted into .csv files. These were then independently run through MaxEnt, allowing for a test to compare the environmental niche of the two national populations of Amur leopard. The aim of this test was to see if the two Amur leopard populations surveyed separately to date occupy the same niche or distinct niches.

MaxEnt models built using localities from the LLNP and surrounding areas of the RFE did not accurately predict the current known locations of leopards within north eastern China, with many described as unsuitable. The equivalent model using only the Chinese points was more successful in predicting the Russian known locations, however many of these latter were still considered unsuitable in this case. This could suggest a difference in ecological niche between the RFE and north eastern China, despite movement between the habitats being documented.

The previously described movement between the RFE and north eastern China would suggest that individual leopards can exist in both national entities despite a potential difference in ecological niche (Wang *et al.,* 2016). Using a combined dataset for the model will enable both components of the Amur leopard's ecological niche to be considered. This model will best represent the potentially suitable habitats in both Russia and China. Each layer was opened in ArcMap and using the 'mosaic to new raster' with the mosaic method set at 'MAXIMUM', therefore showing all areas predicted by both models. 147 presence records were used for training and 48 for testing with 10147 points used to determine the MaxEnt distribution.

2.6.5 The Siberian Tiger MaxEnt Model

The movement and presence of the Siberian tiger within north eastern China has long been unsure, but modern knowledge confirms their presence in areas along the border with Russia (Wang *et al.,* 2016). The occurrence data gathered for this study lacked significantly in Chinese points and therefore any model would be skewed towards the environmental makeup found in the RFE. This was confirmed when all points were run through MaxEnt. Only small areas of suitability, all in close proximity to the Russian border, were considered suitable. Data from Xiaofeng *et al.,* (2011), which was collected in 1998 and 1999 represented the only data away from this border in China. The age of this data caused concern but it was tested against the IUCN geographic distribution of the Siberian tiger, which showed the range as of 2006, and all point locations fell within this range. An original run through of the model in maxent discovered two large areas to be considered highly unsuitable however, Siberian tiger occurrence in these areas is known (exact location data could not be found here, only descriptions of sightings were found). To attempt to overcome this, IUCN-derived pseudo-locality data, for this area, was merged with the occurrence data gathered from the literature and run through MaxEnt to create the final maximum entropy model for the Siberian tiger. To do this, the large continuous area stretching across the border of China and Russia was split into 200km^2 grids (tiger home ranges, as suggested by Wilson and Mittermeier (2009b)) with a single random point placed in each grid cell.

The undesirable use of pseudo-locality data in a suitability model is understood and was only selected to be used due to the small dataset of occurrence points. It is understood that this area exists as an important part of the Siberian tiger's distribution. It must also be stated that the output model of this study is not a final answer to Siberian tiger conservation. Instead it aims to present some new ideas and areas that may have potential for future work, meaning that further analysis of each area is fundamental.

From the MaxEnt analysis 458 presence records were used for training and 152 for testing, with 10458 points being used to determine the MaxEnt distribution.

2.6.6 Human Disturbances Model

A single human disturbance model was created in ArcMap 10.5.1 to display the level of human disturbance in each grid cell in the big cats' range and give an idea of how fragmented current and future suggested ranges are by major roads, cities and towns.

The Global Human Influence Index (HII) (WCS, 2015) was used as a basis with this displaying all anthropogenic features that could act as disturbances and which can thus be actively avoided when suggesting suitable areas. The presence of a road through the middle of a habitat acts as a major cause of fragmentation. Many animals will not cross roads and if they do so can often result in death or injury, this as well as roads being linked to poaching (To be discussed further in chapter 4). Therefore, for this model, roads are being exaggerated. Using the CIESEN (2013) road map, a 2km and a 5km buffer zone was constructed around all major roads, as done by Hebblewhite *et al.,* (2012). All areas within the 2km buffer were ranked as extremely poor habitat and so be avoided in conservation planning. Areas within the 2-5km buffer were considered good habitat by Hebblewhite *et al.,* (2012) however, for this study they are also considered poor habitat as this will further reduce the chance of encountering roads and humans.

The HII displayed on a continuous scale from 0-1000, with 1000 being the areas with the highest human influence. Using the 'raster calculator' the areas within the 2km buffer were given a value of 500 and areas within the 2-5km buffer given a value of 300.

The resulting road and human impact layers were then combined using the 'mosaic' tool using the MAXIMUM mosaic method. Maximum was selected as both this allows for both variables to always be represented, an average would result in a lower value when one variable is low however, this is still a threat and should still be considered so. This combined human disturbance model was then used to determine the levels of fragmentation for the areas of potentially suitable habitat identified by MaxEnt models for each species. This enables the avoidance of areas which are climatically or environmentally suitable, but which experience large amounts of anthropogenic disturbance that would prevent tiger or leopard colonisation. Using the natural break (Jenks) method, the combined human disturbance model could be naturally subdivided into 4 habitat types: Extremely suitable (low disturbance, so a combined human impact score of 0-221), somewhat suitable (221-442), suitable (442-664) and unsuitable (664-1500). This enabled potential reintroduction areas to be easily checked for anthropogenic factors that might affect their use by large cats.

2.6.7 Prey Modelling

Two prey models, one per big cat taxon, were created in ArcMap 10.5.1 on separate blank projects. IUCN Red List distribution features for each of the predators' prey species were uploaded to the project. Each feature was then converted to a raster using the 'feature to raster' tool, displaying presence as a value of 1 and using the default cell size (0.008333˚). These features were then clipped to the default extent of the other models.

Using the raster calculator, the key prey for each of the Amur leopard and the Siberian tiger were given a cell value of 1. Subsidiary prey values (Table 4.) were calculated using the equation:

$$^{pw}/_{Pw}$$

$pw = \text{Average prey weight}$
$Pw = \text{Average predator weight}$

The average prey weights calculated from minimum and maximum weights gathered from Wilson and Mettermeier (2009; 2011; 2016). Each subsidiary prey raster was then given its respective value, again using the 'raster calculator'. To create the two prey models, all prey raster layers were combined using the 'mosaic to new raster' using the mosaic method 'SUM' therefore displaying the total prey value for the area. All values below 2 were grouped with these areas described as unsuitable, this being suggested by Miquelle *et al*. (1999) where tiger distribution in the RFE is associated with the combined presence of two key prey species therefore anything less will not suitably sustain a population. This assumption is also used as a proxy for the Amur leopard across the full range. This model can then be combined with habitat suitability model and human disturbances model giving a prey value, demonstrating the variety of available prey. This model does not take into account abundance, just range, this is something that could offer a possible continuation from this study.

*Table 4. Prey species of both the Amur leopard and the Siberian tiger with their average weights calculated from values given in Wilson and Mettermeier (2009; 2011; 2016). Values are calculated using the above equation. *Wapiti calf is shown as adults are considered prey for Siberian tigers but calves were chosen to best represent wapiti in the Amur leopard diet. **Wild boar is considered a key prey source for the tiger but not for the leopard due to size and danger associated with adults, therefore the average weight was calculated using the occurrence of wild boar dietary analysis (Yang et al., 2018) this would therefore represent the average weight of wild boar preyed upon by the Amur leopard . *** Moose importance for the tiger was calculated using the sum of the percentage importance within dietary analysis (Miquelle et al., 1996). The symbol n/a represents those species that are not included in the respective predator diet.*

Prey Species	Avg. Weight (kg)	Amur Leopard Value	Siberian Tiger Value
Eastern Roe Deer	41.0	**1**	0.228
Sika Deer	80.0	**1**	**1**
Musk Deer	12.0	0.261	0.067
Wapiti	14.0	0.304 (Calf)*	**1**
Wild Boar**	13.9**	0.303	**1**
Moose	200.0	n/a	0.164***
Raccoon Dog	7.7	0.168	0.043
Asian Badger	6.3	0.136	0.035
Mountain Hare	2.9	0.063	n/a
Manchurian Hare	2.0	0.043	n/a
Red Fox	8.5	0.185	0.047
Eurasian Otter	9.5	0.207	n/a

2.7 Carrying Capacities

2.7.1 Introduction

The carrying capacity, as discussed in 1.11, can be determined as an "environment's maximal load", or the number of individuals of a single species that a habitat can support (Hui, 2006). This ecological function is particularly important when discussing large carnivores. A population of carnivores that is above the carrying capacity of a region can cause a detrimental effect on the communities of the ecosystem, with prey species becoming over exploited (Hayward *et al.,* 2007). With predator reintroductions, establishing the theoretical carrying capacities of potential new habitats will help to analyse their success rate and how this area will benefit the species as a whole.

By obtaining carrying capacity estimates for each suggested region, the potential impact of this study can be given as a numeric population increase value. This will also help us better assess the potential for conservation impact that the suggestions made by this study could have.

2.7.2 Carrying Capacity Estimates

The estimations for the carrying capacities of each suggested region will be given as a mean value (+SD) of various carrying capacities, density estimates and territory sizes gained from other sources. This synthesis of information will combine many methods for obtaining a carrying capacity, therefore the mean of these may give a more precise prediction than any single estimate can alone. It must also be noted that each of the different predictions occur in different parts of the ranges of the Siberian tiger and the Amur leopard, where the quality of habitat differs. Therefore, with values coming from areas of different quality an average will represent the diversity of habitat qualities across the species' ranges and avoid over- or underestimates that might result from selecting an unrepresentative area as a source of density measures. Averages will also be calculated using both male and female territory sizes, despite both male tigers and leopards having considerably larger territories than the females of the species. This will show the average ranges of the species rather than male and females individually.

It must however be noted that these values can never be taken as definite: they are discussed as estimations, to demonstrate the potential that this study has for the future conservation of Siberian tigers and Amur leopards. For the purposes of making these estimates it is also assumed that all individuals have a territory of the same size that fits into the region suggested. These population estimates do not consider habitat suitability. It can be assumed that a habitat of higher suitability would result in individuals having a smaller territory as resources are more abundant hence, work on ensuring that habitat is of the highest quality would make these population estimates underestimates and might increase numbers slightly beyond what is suggested here.

Chapter Three: Results and Discussions

3 .1 Amur Leopard Model Results

3.1.1 Amur Leopard Habitat Suitability Model

The Amur leopard suitability model shows potential for 22,116 km^2 of suitable habitat areas, that have potential for the release and establishment of a new population (Fig 4.) across the species' historic distribution. Stein *et al.,* (2016) noted that this historical

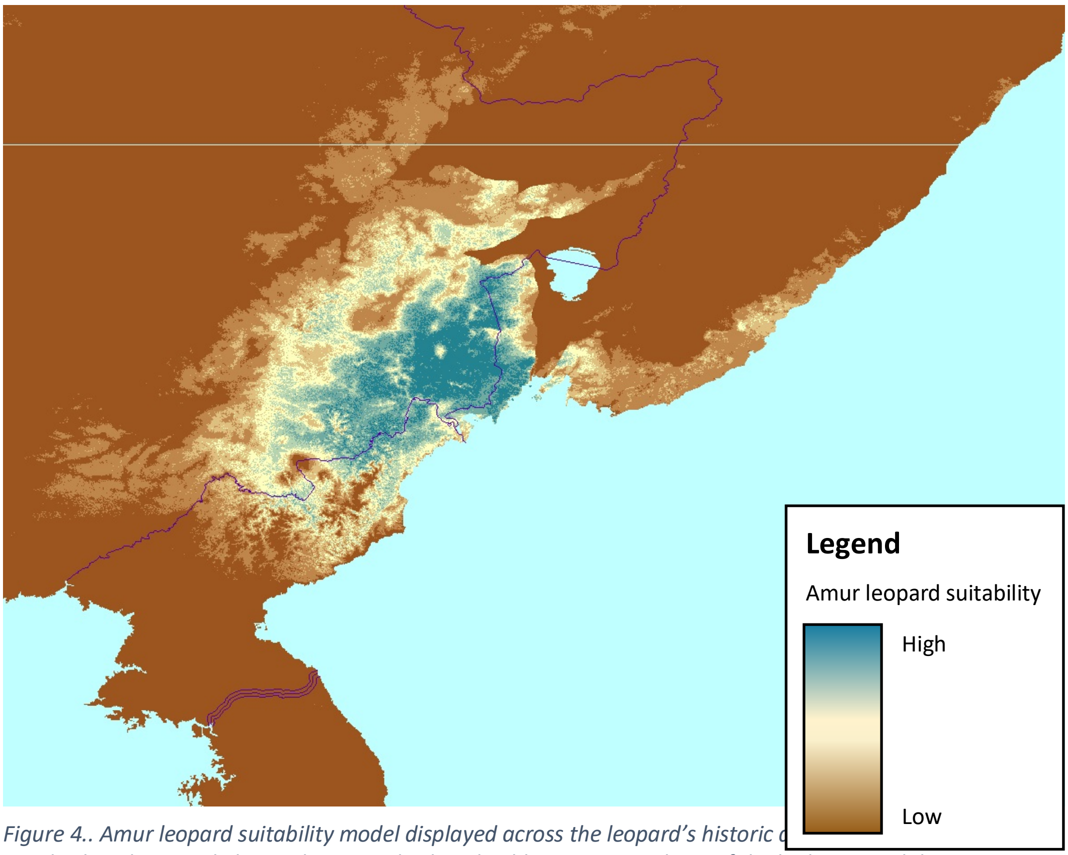

Figure 4.. Amur leopard suitability model displayed across the leopard's historic d
are displayed as purple lines. The areas displayed in blue represent those of the highest suitability.

area spans a total of 435,038km^2 but suggested that only 5.08% of this is currently suitable for the leopard. Just over 12,000 km^2 of current occupied Amur leopard habitat exist (Stein *et al.,* 2016) and therefore could increase their range by 181% to 34,322km^2.

When analysing the suitability of current locations as assigned by the model created, many of these current locations were considered of low suitability values ($\mu = 0.615 \pm 0.123$). Therefore, this model suggests that some current populations may be existing in areas not considered to be of optimal or high habitat suitability. The maximum test sensitivity plus specificity threshold gave a logistic value of 0.056. Using this threshold value, along with the mean value for current location points, 3 classes were created: 0-0.056 (unsuitable), 0.056-0.615 (moderately suitable) and 0.615-1 (highly suitable). For selection of suitable areas, a cut-off point off 0.417, the minimum value not considered an outlier, was used. Although this value is considered outside the suitable classes and hence not optimal, it demonstrates areas of which are proven to currently have leopards and therefore values above this can be considered as having potential for Amur leopard populations. The model displayed an AUC of 0.989 ($\pm$ 0.002), suggesting high performance and increasing the likelihood of the suggested regions being suitable for the leopard.

The potential reintroduction area selection followed a set criterion. Each suggestion must be within the historic distribution of the species. If an area has an occurrence point, then this area, up till the point of a barrier, is considered current habitat. Human disturbance value was kept to a minimum. Areas that are considered extremely unsuitable which are around roads and cities, are actively avoided. Areas with considerable distance from other suggested areas or the current distribution were ignored as no corridor between would be achievable.

By merging the human disturbances model and suitability model, continuous areas with minimal human disturbances could be identified and selected. This modelling has identified 18 new areas being found which are suitable for the Amur leopard (Fig 5). Although currently fragmented, these areas can be separated into 4 larger regions (Table 5). The first is located near the Ussurisky nature reserve, RFE, and consists of two areas, the second and largest stretches over an area of Heilongjiang, north east China, and across the border into western regions of Primorski Krai, RFE.

The third region exists in the Jilin region of China and stretches into parts of North Korea, this is made up of 6 smaller areas. The final region is also located in the Jilin region. This region stands alone from other suggested areas however, it is in close proximity to the current distribution of the leopard with human induced fragmentation between existing and potential new areas the main obstacle to expansion. Therefore, this could act as an extension of already known habitat, with the correct conservation requirements and assuming that conservation is prioritised. These regions all fall within the moderately suitable class, which is considered a similar suitability to the majority of current Amur leopard range. Large fragments of highly suitable habitat are also present, offering the optimal habitat which is considered to be of a higher quality than most of the current known range.

The areas containing the largest amount of highly suitable leopard habitat are those across the Chinese-Korean border along with the suggested area on the Russian-Chinese border, west of Lake Khanka. The other areas suggested contained varying levels of highly suitable habitat but were considered moderately suitable almost in their entirety.

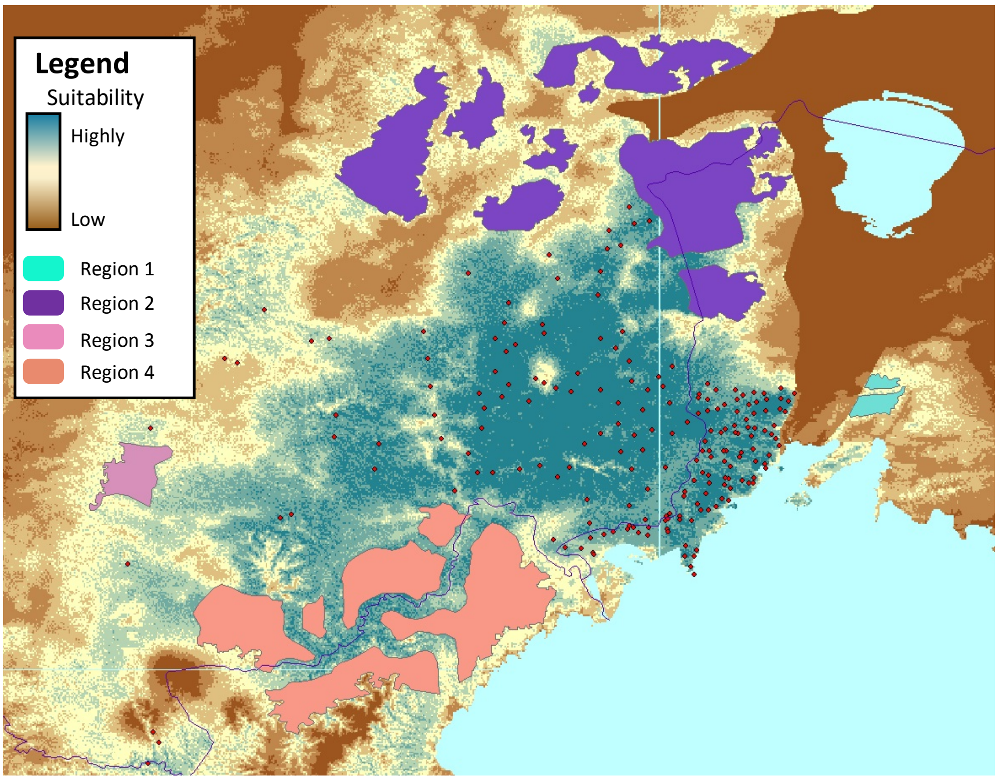

Figure 5. Habitat suitability for the Amur leopard. Each suggested area has been grouped with nearby areas into 4 larger regions. Region 1: Ussurisky. Region 2: Heilongjiang-Primorski Krai. Region 3: Jilin. Region 4: Jilin-North Korea. The occurrence data for recorded Amur leopard occurrence are shown in red and areas in blue represent the highest habitat suitability based on the model.

Table 5. Classification of the potential areas for Amur leopards, split up into the larger regions. The size and combined sizes of each are given. The average human disturbance across the whole area is also given with the modal value also provided. The mean value will include edge habitat that will have higher human disturbance values than the area centres therefore the mode gives a better representation of the level of human disturbance.

Region	Region Size	Area	Size (km^2)	Human Disturbances Mean Value	Human Disturbances Modal Value
Ussurisky	384 km^2	1	114	0.253	0.128
		2	270	0.196	0.128
Heilongjiang-Primorski Krai	11,714 km^2	3	82	0.156	0.149
		4	2096	0.177	0.149
		5	740	0.181	0.191
		6	2437	0.205	0.191
		7	45	0.196	0.149
		8	338	0.180	0.149
		9	896	0.201	0.191
		10	4073	0.157	0.149
		11	1007	0.190	0.191
Jilin	869 km^2	12	869	0.205	0.191
Jilin-North Korea	9149 km^2	13	1560	0.197	0.191
		14	3186	0.189	0.191
		15	230	0.174	0.149
		16	421	0.215	0.191
		17	1908	0.187	0.149
		18	1844	0.178	0.149

3.1.2 Amur Leopard Sensitivity Analysis

When constructing the Amur leopard niche model in MaxEnt, the biome variable was the most important to identifying the leopard's suitable habitat (contributing 34.2%). The 3 next most important variables were annual mean temperature (19.9%), temperature seasonality (17.4%) and precipitation seasonality (14.5%). Together these make up 86% of the variation within the suggested habitats (See Appendix 1 for further information).

Jackknife analysis of the model gives a better understanding of variable importance and so was also used. When used in isolation, temperature seasonality proposes the highest gain and therefore appears to represent the most important variable. Temperature seasonality also has the largest effect on gain when it is omitted, although this is not substantial. This suggests that while temperature seasonality has the most information when ran alone, it also has the most information that is not present in the other variables used. Despite showing the most effect, there is no substantial difference between each variable, therefore omitting each does not decrease the training gain considerably enough. Jackknife of test gain shows variation, annual precipitation and temperature seasonality jointly appear as the most important scores. This would suggest that while temperature seasonality obtains a good fit to all training data, annual precipitation will give better results when used on test data alone. The analysis shows that the exclusion of any variable would decrease the predictive performance of the model.

The biome which the Amur leopard appears most sensitive to and actively seems to select for is the temperate broadleaf and mixed forest. The flooded grasslands and savannas biome, part of the RFE that intersects the temperate broadleaf and mixed forest biome, is identified by this model as unsuitable habitat for the leopard, along with the boreal forest biome. From the 3 continuous variables considered the most important to Amur leopard habitats, the annual mean temperature reaction norm suggests that the most suitable habitats are around 5°C. The optimal temperature seasonality score for leopard habitat is approximately 1150 and the precipitation seasonality optimum was ~80. The annual precipitation is optimal at ~700mm. The model suggests that the optimal altitude for leopards is ~300m. Slope is optimum at ~11°. Slope aspect is considered least suitable at north facing degrees, as was expected. The index of human impact is considered optimum at low levels of disturbance however areas with almost no disturbance are considered to be unsuitable for the leopard. As expected, areas of high disturbance are also considered to be unsuitable. (Please see appendix for response curves demonstrating the response of each variable).

3.1.3 Amur leopard Prey Model

The inclusion of this prey distribution model gives a single value for the abundance of prey within the suggested areas (Table 6). All 18 areas have a prey value above the 2.00 discrimination value and so have capability to support populations of Amur leopard, upon further localised research into prey movement, their abundance and placement within these areas.

Table 6. The prey communities present in each of the areas and their respective regions. The average prey area for each area is also provided. A ✓ represents their presence and, a ✗ represents their absence.

	Prey species	Badger	Wild boar	Wapiti	Sika deer	Roe deer	Red fox	Raccoon Dog	Otter	Musk deer	Mountain hare	Manchurian hare	Avg. prey value
Region 1	1	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.669
	2	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.669
Region 2	3	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	4	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	5	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	6	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	7	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	8	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	9	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	10	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	11	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
Region 3	12	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
Region 4	13	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	14	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	15	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	16	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	17	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606
	18	✓	✓	✓	✗	✓	✓	✓	✓	✓	✗	✓	2.606

The Eastern roe deer is present throughout all 18 of the suggested areas, whereas the Sika deer is not currently present in any area. There are however many of the leopard's subsidiary prey species, which this model suggests may make up for this deficit. The 2 areas within the Ussurisky nature reserve have an average prey value of 2.669, which represents 72.7% of the available prey suggested in this study. All areas from the 3 larger suitable habitat regions are identical and have average prey value of 2.606 (71% of suggested prey).

Areas moving northwards through Primorskii Krai were considered unsuitable (see figs. 4 and 5) by the suitability model for the Amur leopard, despite being part of its historic distribution. Interestingly, these are also areas where the Siberian roe deer are not present, perhaps offering an insight as to why this is now considered unsuitable for the leopard according to the MaxEnt model above.

3.1.4 Amur Leopard Carrying Capacity Estimates

Synthesis of Amur leopard territories, densities and population estimates suggests an average density for Amur leopards of 0.97 individuals/100km^2 (Table 7). Putting this with the size of the region in the DPR Korea and north eastern China, that Chapter 3 identified as the best zone for leopard reintroduction, the new region could offer potential territories for 89 breeding Amur leopards. This would be almost double what the current population is believed to be at. The synthesis also suggests that the average territory size for the leopard is at 103.1 km^2. While this information is only an estimate, we could envision specific directions for future work using density vs occurrence probability graphs, as used by Jiang *et al.,* 2015. If higher-quality density data can be collected from current populations and combined with accurate suitability models, created using current data from monitoring programmes, population estimates could be made even more precise and hence of even more benefit to the conservation actions proposed. At present, however, it suffices to note that even a rough estimate suggests the area identified in this study could double the global, wild Amur leopard population.

*Table 7. Synthesis of Amur leopard densities used to determine a population estimate for the suggested region. The region totals an area of 9149 km^2. These densities are calculated, by myself, from suggested populations and the study area in which the populations occur. *The smallest suggested range of a female Amur leopard. ** The suggested average range of a male Amur leopard. *** This density is calculated from 11292 km^2 of current, known Amur leopard range. **** This density is calculated from 21173.7 km^2 of potential Amur leopard range.*

Citation	Density (per 100km^2)	Population Estimate
Wilson and Mittermeier, 2009a	2.1*	193
	0.36**	33
Wang *et al.,* 2007	0.36	33
Qi *et al.,* 2015	0.62	57
Augustine *et al.,* 1996	1.81	166
Wang *et al.,* 2015	0.7	64
Hebblewhite *et al.,* 2011	0.97	89
Jiang *et al.,* 2015	0.89***	81
	0.92****	84
Average	0.97	88.8

3.2 Siberian Tiger Model Results

3.2.1 Siberian Tiger Suitability Model

The suitability model created in MaxEnt for the Siberian tiger showed potential for 29,666 km^2 of further habitat that could be considered for future reintroductions and the establishment of new populations (Fig. 6). This new habitat is largely within the historic distribution proposed by Goodrich *et al.* (2015) as part of the IUCN Red List assessment of the species, these areas also exist within the historic distribution put forth by Tian *et al.* (2011). If we assume the current distribution suggested by Goodrich *et al.* (2015), these new areas would increase suitable tiger habitat by 31%.

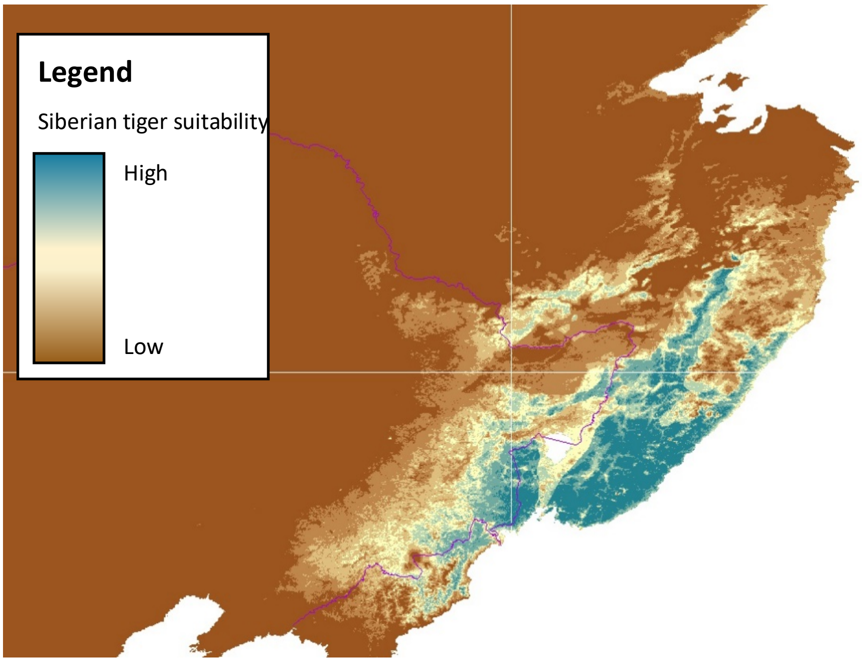

Figure 6. Siberian tiger suitability model displayed across the tiger's historic distribution. Country borders are displayed as pink lines. The areas displayed in blue represent those of the highest suitability.

Comparison of the current known locations of the Siberian tiger with the suitability model showed a large variation ($\mu = 0.670 \pm 0.203$) demonstrating that many current areas are not as suitable as would be advised. The threshold value, maximum test sensitivity plus specificity, gave a logistic value of 0.086, again reinforcing the point of poor current habitat suitability. 3 classes were created which allows for classification of the suitable habitat suggested, these were created from the threshold value and the mean (Fig. 4): Unsuitable (0-0.086), moderately suitable (0.086-0.670) and highly suitable (0.670-1). For the selection of areas that could act as future habitats for the Siberian tiger, a cut-off value of 0.640 was selected, this being the lowest current location suitability value not considered an outlier. Any area above this value therefore has evidence that tigers can survive here and so can be considered to varying extents as future habitats. The high performance of this model, AUC of 0.962 ($\pm$ 0.003), demonstrates the effectiveness at selecting those areas which can be considered suitable for the Siberian tiger.

As with the Amur leopard, the selection of potential area followed a set criterion. Each area must be within the historical distribution of the Siberian tiger, put forth by both Goodrich *et al.* (2015) and Tian *et al.* (2011). All areas with an occurrence point present are considered current habitat up to the point of a barrier. Human disturbance values are kept to a minimum, actively avoiding the extremely unsuitable class and finally, only areas around the current distribution of the tiger or near other suggested areas are considered. Any areas away from others would be fragmented and so unable to support a sustainable population.

The inclusion of the human disturbances model allows for the creation of areas away from human disturbance. The combination of this model along with the suitability model led to creation of 25 areas considered suitable for future Siberian tiger populations (Fig 7.). These 25 areas, currently fragmented, can be grouped into 4 larger regions (Table 8). The first regions encompass areas within 2 Russian krais (federal subjects), Khabarovsk Krai and the Jewish Autonomous Oblast (JAO). Made up of 7 areas with a total expanse of 6,618 km^2, these areas all exist within the temperate broadleaf and mixed forest biome. Despite once being present, the Siberian tiger has since been extirpated from this region (Miquelle *et al.,* 2015). The second region is the largest of the four. The total area of this region is 13,967km2, made up of 10 smaller areas and exists across the Primorski Krai-Heilongjiang border. The third region is across the Jilin-North Korea border and is made up of 6 areas. The final region is within Primorski Krai. This region is not included within the IUCN current distribution, but current location points were included within this study. These points however, were collected from a study in 1998-1999 and do not match up with the

IUCN current distribution (All other from the study is within the IUCN current distribution). The inclusion of this region will allow for further research to discover if tiger presence is there and if not, the possibility of using it as a future area can be determined.

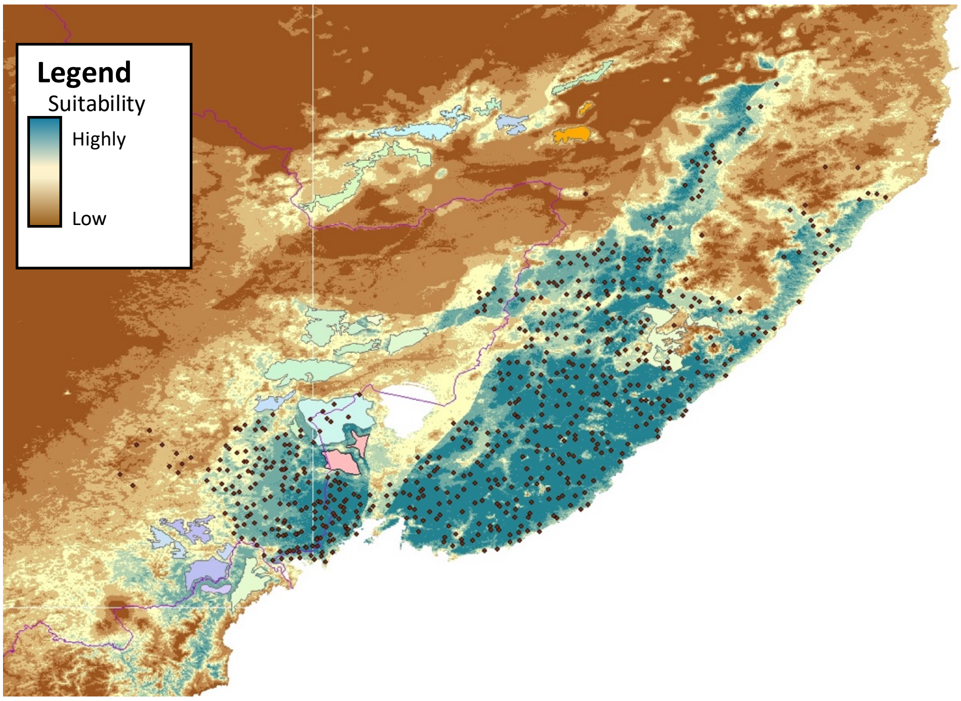

Figure 7. Habitat suitability for the Siberian tiger. Each suggested region is demonstrated in block colour. The areas can be visibly grouped into 4 separate regions based on their location. Region 1: Khabarovsk Krai-Jewish Autonomous Oblast. Region 2: Primorski Krai-Heilongjiang. Region 3: Jilin-North Korea. Region 4: Primorski Krai. Areas in blue represent the highest habitat suitability based on the model. Brown dots show the location points collected and used in this study.

Highly suitable Siberian tiger habitat mostly occurs within its current distribution, however areas from the Primorski Krai-Heilongjiang region, currently considered to be without tigers, contain the largest areas of highly suitable habitat. This region is also close to the current population to the south, making it a highly valuable option as a future area. Areas within the Jilin-North Korea region also contain highly suitable areas, along with those in the Heilongjiang province of China, considerably close to the existent population. The region within the Khabarovsk Krai-JAO contains the lowest suitable habitat of the 4 regions however, has the lowest human disturbance value. It is the areas within China and Korea that have the largest human disturbance values, they are still considered more suitable and all other areas coming under the highly suitable class.

Table 8. Classification of the suitable areas for the Siberian tiger, these are split into 4 larger regions. The size of each area and region is given in km² along with the mean human disturbances values. The modal value is also given as the gives a better indication of the overall level of human disturbance of the area with some area edges having higher value than those in the centre.

Region	Region Size	Area	Size (km^2)	Human Disturbances Mean Value	Human Disturbances Modal Value
Khabarovsk Krai – Jewish Autonomous Oblast	6618 km^2	1	614	0.039	0.022
		2	767	0.035	0.022
		3	124	0.036	0.022
		4	1766	0.075	0.075
		5	2395	0.059	0.075
		6	307	0.054	0.032
		7	645	0.041	0.032
Primorski Krai - Heilongjiang	13,967 km^2	8	4757	0.151	0.149
		9	1171	0.183	0.191
		10	461	0.157	0.106
		11	698	0.156	0.149
		12	658	0.159	0.149
		13	2700	0.172	0.149
		14	678	0.163	0.149
		15	306	0.169	0.149
		16	1979	0.161	0.149
		17	204	0.150	0.149
Jilin – North Korea	6101 km^2	18	1504	0.192	0.191
		19	1767	0.169	0.149
		20	366	0.202	0.191
		21	419	0.178	0.191
		22	1155	0.158	0.149
		23	890	0.162	0.149
Primorski Krai	2980 km^2	24	2522	0.043	0.054
		25	458	0.025	0.022

3.2.2 Siberian Tiger Sensitivity Analysis

Like the Amur leopard, the variable of which the Siberian tiger appears most sensitive is biomes, making up 39% contribution. The annual mean temperature also represents a large percentage contribution (24%), and along with biomes, precipitation seasonality (19%) and annual precipitation (9%), this makes up 91% contribution of all variables (See Appendix 2 for further information).

Jackknife analysis of training gain for the Siberian tiger shows annual precipitation to be the most important variable when ran in isolation and has the largest training gain of all variables included in analysis. Precipitation seasonality is the variable which, when omitted, decreases the training gain the most, therefore having the most information that is not present in other variables included. Again, this difference is not substantial and therefore the omission of any variable does not decrease the training gain a considerable amount. Jackknife analysis of test gain gives results similar to training gain, suggesting that annual precipitation obtains a good fit to both training and test data.

The temperature broadleaf and mixed forest biome seen throughout the Siberian tiger's current distribution is the biome in which it appears most sensitive. The edges of this biome appear as barriers in many cases, this can be seen with both the marshland biome and other forest biome with both showing as unsuitable habitat. The other forest biome once appeared as historic Siberian tiger distribution but is now considered to be unsuitable. The tiger appears to favour altitudes below ~ 700m. Slope aspect does not differ greatly, with exception of the north facing appearing to be least favoured, slope degree is favoured around 2°. Of the climatic variables, annual mean temperature is optimal at ~ 2.5°. Annual precipitation is optimal at ~ 800mm. Precipitation seasonality shows the highest response at ~ 70 and with temperature seasonality, the highest response is ~ 1180. Finally, the response of the Siberian tiger to the human impact index shows the highest response at ~ 15, this then decreases with high levels of disturbance showing no response. The value of 0 human disturbances shows no response, while a decrease in response is also seen at ~ 4, this could be due to a lack of areas with human disturbances of these values, or possibly that these areas are simply impossible to get to. (Please see appendix for response curves demonstrating the response of each variable).

3.2.3 Siberian Tiger Prey Model

The Siberian tiger prey distribution model allows a value to be given to the variety of prey available within each of the areas suggested by the combined suitability and human disturbances model (Table 9). All areas suggested are above the 2.00

discrimination value and so have the capability, upon localised research into prey movement and occurrence within each area, to support Siberian tiger populations.

The wild boar and the wapiti, two of the Siberian tiger's key prey species, are present in all 25 areas however, the sika deer is not present in any. The other, subsidiary, prey species are available in large numbers, suggesting that there is a variation of prey of which, could support tiger populations. The 6 areas within the Khabarovsk Krai-JAO region show the highest average prey value (2.583). The multiple areas across the Primorski Krai-Heilongjiang region show a slight variation. These values range from 2.419 to 2.583, showing an average of 2.463. The variation within these regions is seen due to the moose. Of the 10 areas, only 2 show moose presence with 1 showing partial presence. The region along the Jilin-North Korea border shows the lowest average prey value of the 4 regions (2.419). The 2 areas which make up the final region, within Primorski Krai, give values of 2.523 and 2.583 (average of 2.553).

Table 9. The prey communities of the Siberian tiger that are present in each of the areas and their respective regions. The average prey value for each area is also provided. A ✓ represents their presence, a ✗ represents their absence and a / represents their presence but not throughout the area.

	Prey species	Badger	Wild boar	Wapiti	Sika deer	Roe deer	Red fox	Raccoon Dog	Musk deer	Mountain hare	Manchurian hare	Moose	Avg. prey value
Region 1	1	✓	✓	✓	✗	✓	✓	✓	✓	✓		✓	2.583
	2	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
	3	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
	4	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
	5	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
	6	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
	7	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.583
Region 2	8	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	9	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	10	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	11	✓	✓	✓	✗	✓	✓	✓	✓	✓	✓	✓	2.579
	12	✓	✓	✓	✗	✓	✓	✓	✓	/	✓	✗	2.435
	13	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	14	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	15	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✗	2.419
	16	✓	✓	✓	✗	✓	✓	✓	✓	/	✓	/	2.516
	17	✓	✓	✓	✗	✓	✓	✓	✓	✗	✓	✓	2.583

Region 3	18	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
	19	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
	20	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
	21	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
	22	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
	23	✓	✓	✓	×	✓	✓	✓	✓	×	✓	×	2.419
Region 4	24	✓	✓	✓	×	/	✓	✓	✓	✓	✓	✓	2.523
	25	✓	✓	✓	×	/	✓	✓	✓	✓	✓	✓	2.583

As expected, suitable Siberian tiger habitat is correlated to the presence of wild boar and wapiti. The most northern areas of suitable tiger habitat also represent the northern limit of both the wild boar and the wapiti, with the moose the only notable prey which is seen further north.

3.2.4 Siberian Tiger Carrying Capacity Estimates

The synthesis of Siberian tiger population estimates suggests that the region in Primorski-Krai and Heilongjiang has potential habitat for 50 (50.2) breeding adults, at a density of 0.38/100km^2 (Table 10.). The region in Khabarovsk Krai-JAO, that was not suggested as a current conservation priority but for future consideration, has potential for 24 (23.8) breeding adults. This could however be an underestimate if the region was to increase in area with future work on habitat quality modelling. Together this suggests homes for 74 additional breeding tigers. This synthesis suggests an average adult tiger range of 263.3km^2, which is close to other findings (Wilson and Mittermeier, 2009b). As with the Amur leopard, constructing density vs occurrence probability graphs would enable more precise estimates to be drawn up and should be a focus of future monitoring and conservation programmes in these suggested areas.

*Table 10. Synthesis of Siberian tiger densities used to determine a population estimate for the suggested conservation priority area in Primorski Krai-Heilongjiang and the region for future conservation consideration in Khabarovsk Krai-JAO. The conservation priority region has a total area of 13,967km² while the future region has an area of 6,618km². *Primorski Krai-Heilongjiang. **Khabarovsk Krai-Jewish Autonomous Oblast. **The male and female densities were combined here as this was from a study in a single study area.*

Citation	Density (per 100km²)	Population Estimate	
		PK-H*	KK-JAO*
Wilson and Mittermeier, 2009b	0.5	70	33
Li *et al.,* 2010	0.25	35	17
Goodrich *et al.,* 2010**	(0.07+0.26) 0.43	46	(5+17) 22
Hebblewhite *et al.,* 2012	0.32	44	21
Wang *et al.,* 2016	0.4	56	26
Average	=0.38	50.2	23.8

3.3 Discussion of Results

The once large forested areas of far eastern Asia have faced many pressures and today only small portions remain (Wang *et al.,* 2016). The Sikhote-Alin mountains, part of these forests, were considered to contain one of the largest densities of endangered species in all of Russia (Cushman and Wallin, 2000). As a result of forest clearing for agriculture, the illegal logging of trees for timber and other natural resource misuses, these habitats are now extremely fragmented (Xiaofeng *et al.,* 2011). The Siberian tiger, moreover, requires extremely large territory sizes. Female tigers with young can require up to 400km^2 of space each, while males can use a range up to 5 times that size, as they attempt to include multiple females within their territory. The largest area put aside by China for tiger conservation, however, is only 1000 km^2 (Li *et al.,* 2010; Xiaofeng *et al.,* 2011). The outlook for Amur leopards is also critical. Only small populations remain in areas of high habitat fragmentation and these have resulted in much genetic inbreeding within the population (Uphyrkina *et al.,* 2002). The need for expanding and developing comprehensive conservation plans for both species, including anti-poaching patrols in areas of human presence (Wang *et al.,* 2016) is urgent or both the Siberian tiger and the Amur leopard could face extinction in the near future.

Today the Amur leopard exists in just over 12,000km^2 of habitat, which is believed to exist within less than 3% of its historical distribution (Stein *et al.,* 2016). With the recommendations made in this study, over 22,000km^2 of new leopard habitat, set up and maintained with strict conservation actions, can be identified. This would raise the total area of Amur leopard habitat to over 34,000km^2 and offering habitat for an estimates 89 adults.

Siberian tigers share 93% of their current distribution with humans (Goodrich *et al.,* 2011) and of this distribution, less than 4% is situated in highly protected areas (Riley *et al.,* 2017). Just under 96,000km^2 of tiger range currently exists, around a third of their historic distribution (Goodrich *et al.,* 2016). With the correct conservation efforts, this study suggests that this current range could increase by almost 29,000km^2, achieving a total distribution area of almost 125,000km^2. These regions could offer habitat for an estimated 50 adult individuals.

3.3.1 Second Order Habitat Selection

We can describe the selection of habitats by species on three levels (Johnson, 1980; Miquelle *et al.,* 1999). The first order describes the geographic range of the species, the second describes the range of habitats incorporated into the range and the third order describes the selection of sites within an individual's territory that represents the critical need of the individual (Miquelle *et al.,* 1999). This study, therefore, helps to understand the second-order habitat selection of the Siberian tiger and the Amur leopard. As third order selection is dependent on the individual animal, this is not something which can be accurately modelled. Miquelle *et al.,* (1999) suggested that habitat type, elevation and slope are all variables that are part of the "decision-making process" for the selection of home ranges and therefore increasing reproductive success. Miquelle *et al.,* (1999) also went on to suggest that tigers select their home range locations to correlate with the presence of their prey. Therefore, the inclusion of a prey variation model, rather than the localised presence of prey, in this work allows for occupied second order habitats to be much more accurately described. The localised movement of prey within these areas along with their abundance will give a better understanding of habitat quality for each individual predator.

3.3.2 Determinants of Suitable Areas

A habitat model can be considered as an answer to a specific question about the relationships between an animal and its respective environment (Mitchell and Hebblewhite, 2012). With maximum entropy habitat modelling, it is presumed that access to preferred resources and ideal abiotic conditions for a species increases its survival and reproductive success. However, this has not been widely investigated with many large carnivores due to the broad absence of long-term monitoring programmes (Guisan and Thuiller, 2005; Hebblewhite *et al.,* 2014) and, to my knowledge, only limited studies have been conducted for either the Amur leopard or Siberian tiger. While many measures of habitat quality seem to assume a direct relationship between the abundance of resources and the density of the target species, this is not always the case. Mosser *et al.* (2009) stated that with lions in the Serengeti, reproductive success was determined by access to areas where prey vulnerability and hunting success were increased. Whereas vegetation and areas of shelter determined lion density and patterns of cub productivity (yearling cubs per km^2). This was supported by Hebblewhite *et al.* (2014) whose modelling of the Siberian tiger habitat found a positive correlation between tiger fitness (numbers of females with cubs) and habitat quality. Hence, habitat quality, through all of its resources, is especially important when considering areas for conservation.

3.3.2.1 Abiotic Habitat Variables – Siberian Tiger

In our models, highly suitable habitats for the Siberian tiger included temperate broadleaf and mixed forest biomes, at mid elevations, with the avoidance of steep slopes and north facing aspects, an average annual precipitation of 800mm and an annual temperature average of 2.5°.

The importance of temperate broadleaf and mixed forest biomes (Fig 8.) corresponds with other studies' findings. It has been suggested that this importance is indirect and comes from the fact that tigers' ungulate prey species rely upon these forest assemblages and hence, make them an important factor for the tiger (Hebblewhite *et al.,* 2011; Hebblewhite *et al.,* 2014). The avoidance of the boreal forest within the RFE found in this study matches the work of Hebblewhite *et al.* (2014). The tiger, along with its prey species the wapiti, the roe deer, wild boar and musk deer, all show a decreased probability of occurrence within the boreal forest biome. These results also support that of Xiaofeng *et al.* (2011), who also found the coniferous (boreal) forest to be ranked outside the most suitable and highly suitable ranks. Despite the findings of this study, along with others, the IUCN, and other descriptions of the tiger's historical distribution, include the boreal forest. This will be discussed further in section 3.3.8.

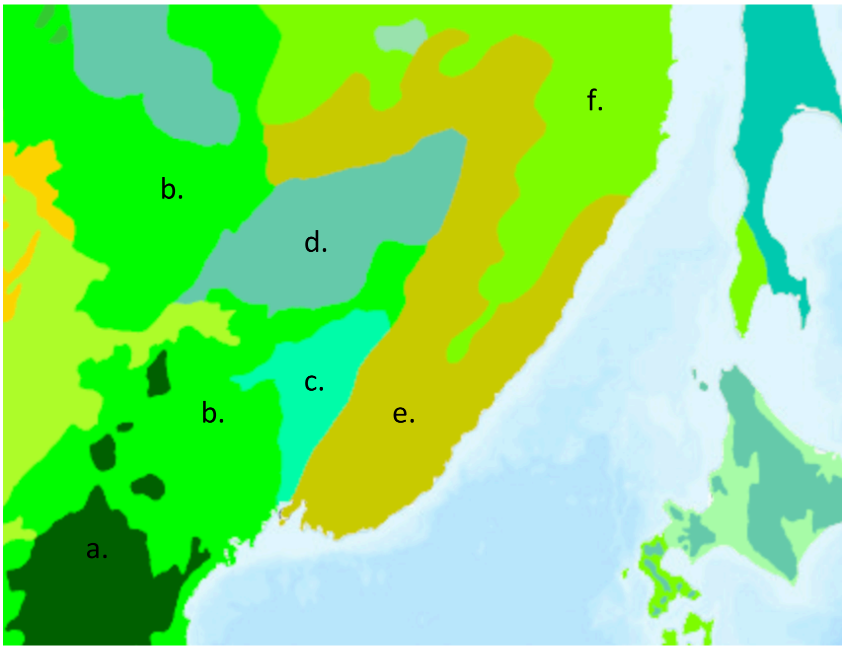

Figure 8. WWF ecoregions of the world across the study area, showing the ecoregions present. a.) Changbai Mountains mixed forests, part of the temperate broadleaf and mixed forest biome (TBMF). b.) Manchurian mixed forests, part of the TBMF. c.) Suiphun-Khanka meadows and forest meadows, part of the flooded grasslands and savanna biome. d.) Amur meadow steppe, part of the flooded grasslands and savannas biome. e.) Ussuri broadleaf and mixed forests, part of the TBMF. f.) Okhotsk-Manchurian taiga, part of the boreal forest biome.

A preference for altitudes below 700m and above 200m above sea level also concurs with other findings, as does the avoidance of steep slopes (Yang *et al.,* 2018; Hebblewhite *et al.,* 2012; Miquelle *et al.,* 1999). South facing slopes, which can be used as an indirect proxy for low snow cover (Hebblewhite *et al.,* 2014), were not found to be a determinant of favourable habitat. However, the avoidance of northerly aspects corresponds with the findings that Siberian tigers avoid areas of high snow cover (Hebblewhite *et al.,* 2012). The bioclimatic variables of habitat quality, as would be expected, match those of the RFE (Goodrich *et al.,* 2010). They allow for the areas outside of the current distribution, but still within the historic range, to be assessed for their ability to act both directly and indirectly as barriers to dispersal. Precipitation can also give a further representation of snow cover, acting as a proxy. Although localised topography can affect snow depth, the amount of average precipitation can aid in the identification of areas that the model will consider unsuitable, mostly to the northern limits of distribution, where snow cover makes prey survival difficult (Jiang *et al.,* 2015).

3.3.2.2 Abiotic Habitat Variables – Amur Leopard

For the Amur leopard, high habitat quality occurs in temperate broadleaf and mixed forest biomes, at mid elevations and with avoidance of steep and north-facing slopes. The optimum annual precipitation is described as 700 m with the annual temperature average of 5°C.

The temperate broadleaf and mixed forest biome is the only biome identified as being suitable for the Amur leopard, which links directly to their prey and the ability to use the forest cover for both hunting and denning (Hebblewhite *et al.,* 2011). This finding mirrors that of other ecological modelling studies, where highly suitable Amur leopard habitat was described as including the mixed Korean pine forests (Jiang *et al.,* 2015; Qi *et al.,* 2015; Hebblewhite *et al.,* 2011; Wang *et al.,* 2016). The Amur leopard does not appear to select for the Ussuri broadleaf and mixed forest, which makes up part of the temperate broadleaf and mixed forest biome. The reason for this is uncertain, however a lack of data on actual leopard occurrence in this ecoregion will have influenced the model's suggested lack of suitability. Areas within this ecoregion have been suggested to be suitable by other studies and so future research in these locations could offer new insights (Hebblewhite *et al.,* 2011)..

The avoidance of altitudes above 1500m by the Amur leopard corresponds with the study by Qi *et al.* (2015) where it was stated that the spruce-fir forests found at these altitudes were avoided. The preference for elevations of approximately 300m differs from previous studies. Qi *et al.* (2015) described the highest quality leopard habitat at intermediate elevations, with a peak at 600-650m. This elevation, along with the intermediate elevations described by other studies (Hebblewhite *et al.,* 2011;

Wang *et al.,* 2016) were not however described as unsuitable by my model. The avoidance of north facing slopes, and hence large amounts of snow cover and depth matches previous studies (Wang *et al.,* 2016; Hebblewhite *et al.,* 2011; Qi *et al.,* 2015; Jiang *et al.,* 2015). Steep slopes are also described as poor habitat quality. As expected, the annual average temperature and annual precipitation, in zones of highest suitability, match that of the Amur leopard's range (Goodrich *et al.,* 2010). As stated with the Siberian tiger, these variables allow for the limits of distribution to be tested, with precipitation also giving a representation of areas of high snow cover which would be unsuitable for the leopard.

3.3.2.3 Biomes as a Barrier - Flooded Grasslands and Savanna

The Suiphun-Khanka meadows and forest meadows and the Amur meadow steppe, which together make up the flooded grasslands and savanna biome, act as natural barriers for both the Siberian tiger and the Amur leopard. The absence of forest, and hence prey and cover, makes this biome extremely unsuitable for both predators. For the Siberian tiger, our finding support those of Xiaofeng *et al.* (2011). For the Amur leopard the complete unsuitability of the flooded grasslands found in this study is not entirely matched by other findings. Hebblewhite *et al.* (2014), for instance, although they did not identify this biome as a key habitat for conservation, found small areas of suitability around the edges of lake Khanka in the flooded grasslands and savannas biome. They do state however, that Amur leopards avoided meadows, which would include those around lake Khanka. Habitat suitability models for the Amur leopard in China do not include the flooded grasslands and savanna biome within their study area, with this likely due to its known avoidance of non-forested areas (Jiang *et al.,* 2015; Wang *et al.,* 2016).

3.3.2.4 Human Disturbance

The results of this study mirror broader scale findings on the effect of human influence on habitat availability for large carnivores. Findings for the cougar (*Puma concolor*), American black bears (*Ursus americanus*), wolverine (*Gulo gulo*) and the Eurasian lynx

(*Lynx lynx*) all identify roads as limiting factors to their dispersal through their respective environments (Dickson *et al.,* 2012; Cushman *et al.,* 2009; Carroll *et al.,* 2001; Basille *et al.,* 2013). Across the entire tiger range, habitat quality decreases with any rise in human impact, with human occurrence sometimes acting as the only consistent predictor for the absence of tigers (Hebblewhite *et al.,* 2014; Linkie *et al.,* 2006). There are studies, albeit disputed, that suggest that tigers and humans can coexist at fine spatial scales (Carter *et al.,* 2012), whereas this study, alongside others, supports the counter-claim that human presence decreases tiger habitat quality (Hebblewhite *et al.,* 2014; Goodrich and Miquelle, 2005).

Unlike tigers, leopards, across their range, do not always show the same level of avoidance of humans. Leopards in Nepal did not avoid humans on foot or in vehicles while inside a national park and were seen to switch to a more nocturnal life style to avoid conflict. This is not consistent throughout the leopard's range, however, with many populations decreasing in density closer to human settlements (Carter *et al.,* 2015). Studies into the Amur leopard's response to humans show a definite avoidance (Hebblewhite *et al.,* 2011: Wang *et al.,* 2016), which is supported by findings from this study. With roads heavily linked to poaching and low ungulate occurrence, these findings, for both the tiger and the leopard, are what was expected and therefore I conclude, which matches many others, that the highest quality habitat for large carnivores exists where human disturbances are minimal.

Checking the response curves for reactions to different levels of human impact, the highest response for both is at low human levels, a human impact of 0 is considered unsuitable for both the Siberian tiger and the Amur leopard, as are some other low values (Fig. 9). This may be due to the areas from which data was collected, with some areas being inaccessible to humans and therefore impossible to test. A further reason for this could be that there are no, or very limited, areas that have 0 human disturbance scores in their respective ranges. This is supported by the statement from Goodrich *et al.,* (2011) that 93% of Amur tiger habitat is coinhabited with humans. It is also possible that these areas are unfavourable for both humans and the cats.

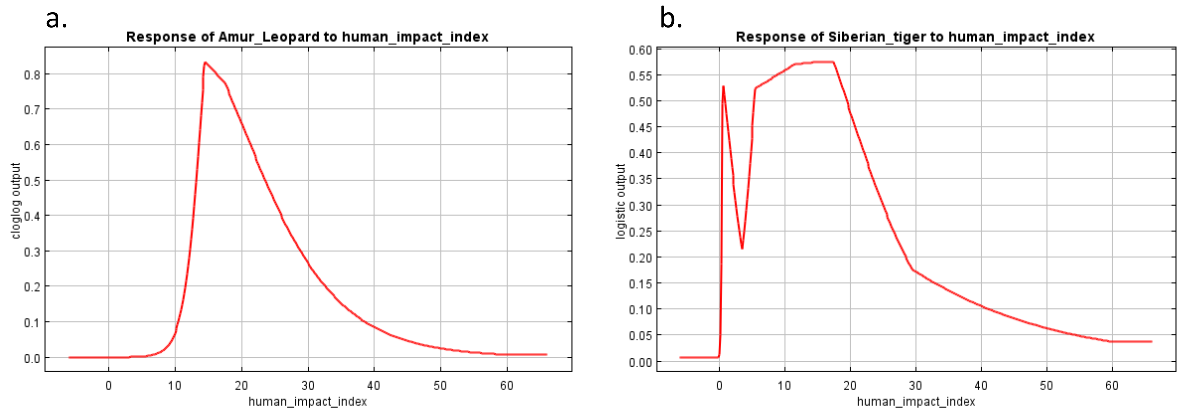

Figure 9. Response of (a.) Siberian tiger and (b.) Amur leopard to human disturbances. Human disturbances is given as the Human Impact Index (WCS, 2015) with the maximum value being 1000. Further response curves can be seen in Appendix 1 and 2.

3.3.2.5 Prey

The Siberian tiger and the Amur leopard are obligate carnivores and so their occurrence, and the suitability of their habitat, will naturally rely also on interactions with their prey. Prey abundances, distributions and habitat areas that enable their predation are all important (Mitchell and Hebblewhite, 2012). Therefore, conservation plans for the Siberian tiger and the Amur leopard would be most effective when they also focus on the habitat of their prey species rather than attempting just to provide high quality carnivore habitat (Miquelle *et al.,* 1996; *Jiang et al., 2015*). The predator occurrence model, created for both species in this study, demonstrates that all suitable areas that should be under consideration based on abiotic factors and prey distributions are above the 2.0 key prey species threshold value suggested by Miquelle *et al.* (1999). This enables the identification of suitable second order habitats. The localised movement of the prey species within these areas, which was beyond the scope of this study, along with their abundance which is not demonstrated by IUCN redlist data should be further researched. This would allow for a more comprehensive, critical analysis of each suggested area’s suitability. The use of these prey occurrence models does give a solid understanding of where the Siberian tiger and Amur leopard have hopes of establishing new populations, with a sufficient quantity of both subsidiary and key prey species available.

The inclusion of subsidiary prey species, to the best of my knowledge, appears to be a first for the Siberian tiger and Amur leopard across their full historic distribution. Prey switching as a result of availability has been recorded in big cats, with examples involving lions in Africa and leopards in Southwest China (Bissett *et al.,* 2012; Johnson *et al.,* 1993). Interactions between the tiger and leopard have also been seen to cause a switch in prey for the less competitive leopard, with them switching to prey sources that differs from areas where there is no tiger presence (Seidensticker and McDougal, 1993). Subsidiary prey species are not only important depending on availability of key prey species, they also represent important prey for various life stages, especially young, old and sick individuals. These must be considered in any plans aiming at the maintenance of a stable population. Their importance of small animals in the diets of large carnivores can often be missed in dietary analysis due to their small size and limited remains, means their exact importance, especially for the young, old and sick can be misinterpreted. Therefore, the inclusion of these subsidiary prey in this study acts as a fundamental step, if plans to establish new, stable populations are to be put into practice.

3.3.3. Assessment of Suitability Models and Caveats

The results from this study mirrors other efforts to find suitable habitats for endangered big cats and other large carnivores. Reintroduction of top order predators is inherently difficult and faces many problems (Wemmer and Sunquist, 1988), with numerous reviews saying it was simply unviable (Stoskopf, 2012). Stories, derived from modelling approaches, have aided in the recovery, expansion and conservation prioritizing of large predators. Suitability modelling for the jaguar in Mexico, for instance, developed a detailed analysis of habitat suitability using environmental covariates, anthropogenic disturbances and prey richness (Rodríguez-Soto *et al.,* 2011), demonstrating the requirement for multiple level inclusion of influential variables. The suitability models created in this study add to the increasing knowledge available to help in the definition of areas suitable for reintroductions of large carnivores.

3.3.3.1. Limitations of the Habitat Models

A debate exists within ecological suitability modelling, with different methods preferred depending on the intended outcome and available inputs. Each also presents their own limitations. Uncertainties do arise from suitability models and must be considered and identified so that the results can be put into context and potential problems can be noted.

There is a possibility that some variables selected and used within this study demonstrate correlation. This can relate in the over exaggeration of these correlated variables' roles in models, causing the modeller to ignore others. Altitude, slope and aspect, as used here, were all calculated from a single digital elevation model using the analysis tools in ArcMap 10.5.1. Although they represent different features, they might thus be autocorrelated. This can give false information on which is the true predictor of occurrence (as it is hard to distinguish the effects of autocorrelated variables from one another), and this can be further problematic when these correlation patterns change over space or time (Braunisch *et al.,* 2013). Each of these topographical features has separately been associated with both Siberian tiger and Amur leopard occurrence and therefore any uncertainty from this should be limited, although not ignored. Xiaofeng *et al,* (2011) suggested that principal component analysis (PCA), a multivariate technique, may be a necessary future step when evaluating Siberian tiger habitat in north eastern China. This would enable sets of correlated variables to be transformed into smaller datasets of independent scores, thus restricting the over-exaggeration caused by correlation. Although this would help reduce the effect of correlation and its underlying problems, this may also give false representation of suitable habitat for both the Siberian tiger and the Amur leopard. In particular, the Amur leopard currently exists in a very small area and so correlation that may be seen in this limited range may not be true across the full historic or the true suitable habitats. The trial use of PCA would definitely help towards gaining the full picture for both species, but it should be used with caution in these small areas, in conjunction with other modelling techniques.

While modelling techniques that use both presence and absence locality points are considered by many to produce more powerful models with higher accuracy

(Brotons *et al.,* 2004), a presence only modelling technique was selected for this study. Using a distribution of locality points as presence points to explore potential further areas, or ecological niche factor analysis (ENFA) as it is widely called, enables the creation of high performance models (Hirzel *et al.,* 2002). Absence data will set locations as unsuitable for the target species and hence, if inaccurate, can heavily influence model outcomes. Absence from areas can also be due to an unknown variable not included in the model and so produce inaccurate correlations between variable (Hirzel *et al.,* 2001). Stockwell and Peterson (2002) suggested the use of pseudoabsences in areas where the target species is not apparent, however this can easily result in bias, especially when, as with the Siberian tiger and Amur leopard, presence data is scarce (Brotons *et al.,* 2004). Furthermore, the elusive nature of both carnivores can make their detection extremely difficult and hence locations that appear as absences may not be and it may just be due to the species remaining hidden. The use of a presence only method is considered better for ecological interpretation and also, as in the case of these two predators, when data is limited with definite absences unsure (Hirzel *et al.,* 2001). Zaniewski *et al.* (2002) also states that presence only modelling techniques are more likely to predict potential distributions that closely resemble the fundamental niche. In species that are not using all the habitats that correspond to their realized niche (to be discussed further in section 3.3.3.2), which can be especially apparent in rare species, ecology may also be better captured using presence only models (Hirzel *et al.,* 2001). While presence only modelling techniques allow for the questions and aims put forth by studies like this one to be addressed, for a higher performance model in localised areas, accurate absence data should be gathered and verified. This can be done using this model put forth by this study, investigating areas suggested for occurrence, while also confirming that areas predicted as unsuitable are areas that can confidently be described as absence locations.

Assumptions are made when creating suitability models that should be tested before conclusions can be validated. These assumptions rely upon higher densities of Siberian tiger and Amur leopard existing in preferred areas and the environmental variables used being consistent with the time at which occurrence data was collected. While this study cannot validate the relationship between densities and preferred areas, this is something that should be considered in further studies, potentially through investigating reproductive success and resource use (Hebblewhite *et al.,* 2011). Snow depth, a variable often associated with both predator and prey occurrence in the study area, was omitted, due to its varying nature with each season and its correlation with north facing slopes. This study is also limited by the resolution of available maps for each of the environmental variables. When investigating suitable areas suggested by this study, localised research into topographical and vegetation variables can aid in the validation of these areas as suitable for populations of Siberian tiger and Amur leopard.

This study offers the first, to my knowledge, suitability model for both the Siberian tiger and the Amur leopard across their full historic distributions, as suggested by Hebblewhite *et al.* (2011), with areas of low human activity prioritized. The studies previously conducted in certain regions of this distribution give an excellent understanding of the current situation of both species and provides options that can be considered for future conservation work. However, many studies omit some regions that are actually diverse. Often modelling work done in the RFE or north eastern China are done independently. A comprehensive model including both would thus help conservation efforts considerably. The inclusion of North Korea in the suitability modelling of these species is extremely limited and while up to date and precise environmental and locality data may not be available for this country, it still remains a potentially important area for both species.

Leopard occurrence and abundance in relation to tigers differs massively dependent on the target area. Tiger presence has been used as a modelling variable for the Amur leopard suitability (Wang *et al.,* 2017). This study did not include tiger presence as a variable inputted into the leopard suitability model. The current populations of both Siberian tigers and Amur leopards are not at healthy and sustainable levels and therefore the exact ecological relationship between them cannot be confidently and accurately assessed. Section 3.8.1 will investigate this competition and relationship further, identifying which of the suggested regions offer the best potential for each species where competition can be limited.

3.3.3.2 Ecological Niche Analysis

Species distribution models (SDMs) aim to predict the current distribution of a species and identify areas that are considered suitable for them through extrapolating their individual ecological niche. This is achieved using predictor variables or dimensions of the environmental space. It is common opinion in the scientific community that these models can only measure the realized niche of the species (Hirzel and Le Lay, 2008). The creation of these SDMs using observation data will include the effects of biotic interactions as background data. and hence will only provide information regarding the realized environmental niche (Pearson *et al.,* 2007).

The realized niche predicted by the respective suitability models constructed here does increase the current range of each of the study species, but is still only a fraction of the historical distributions. With human impact and disturbances largely blamed for the decrease of each of the predators, this could suggest that a shift of the realized niche has occurred, or that a reduction of the niche has occurred because of this change in ecosystem variables. A shift in the niche can occur as a result of speciation events or climatic changes (Pearman *et al.,* 2007). While certain areas of the historic distribution may not have current populations, they may still offer regions in which could offer much suitable habitat for future populations. A niche shift can be measured through hindcasting, the forecasting of current distributions using models which are fitted using historical data (Pearman *et al.,* 2007). This would reveal the extent of the shift and may aid in the identification of further areas that would benefit the conservation of the Siberian tiger and the Amur leopard, along with other endangered species that have suffered from range contraction.

Areas of 0 human disturbance are widely recognised as being best for top mammalian predators. However, both the suitability model for the Siberian tiger and the Amur leopard show these areas as unsuitable. This demonstrates how the range of both has changed but can also give insight into why the true niche of both is not displayed. While anthropogenically-induced pressures may have caused the contraction of their respective ranges along with determining the range of both species, areas unaffected by these pressures that may still offer suitability will have no representation in the model (Fig. 10). This could be heavily influenced by the reason for extirpation from an area. If the ecosystem has become unsuitable due to a change in climatic conditions, habitat loss or increase in human impact, then they would likely still be considered unsuitable. If the reason for extirpation is due to further causes like a loss of prey, hunting (not always linked directly to an increase in human impact), or a genetic bottleneck catastrophe, then the potential for the reintroduction into these areas may exist, with the right prior actions. Hence, the mechanics of extinction should always be considered with suitability modelling.

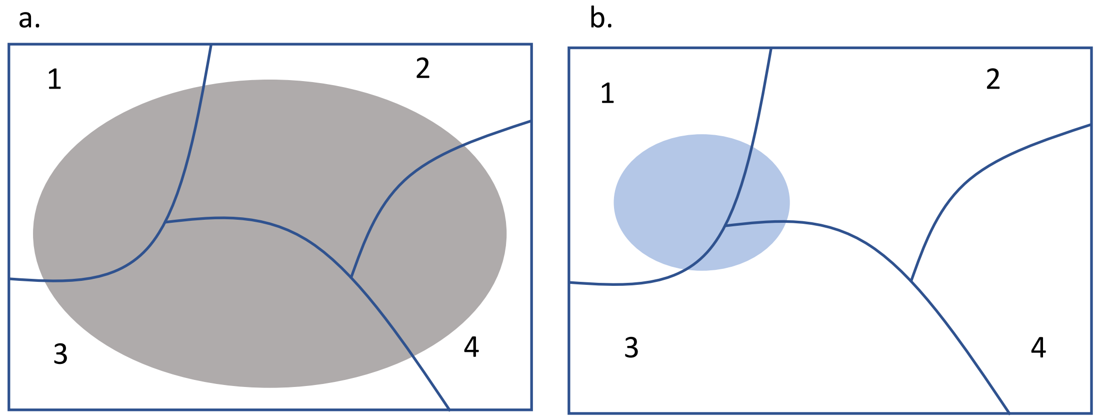

Figure 10. The historical (a.) and current (b.) distribution of a fictional species. Numbers 1-4 represent different ecosystems. (a.) The historic distribution of this species includes all 4 ecosystems in the region and therefore includes variables for each of the respective ecosystems. (b.) The current distribution of this species now only exists in ecosystem 1,2 and 3 and hence, the variables that exist in ecosystem 4 will not be considered in any suitability model. This figure is a simplistic view to aid in understanding.

To best assist any endangered species through suitability modelling, various niche dynamics should be considered and further researched. Few studies exist investigating niche interactions and their evolution (Hirzel and Le Lay, 2008). Creating models using species data that directly links to the fitness of the species would help with the identification of the true realized niche. Using kill sites, hunting sites, and denning sites among others would benefit immensely the creation of suitability models and should be the focus for future occurrence studies for both the two species included in this study, but also for all suitability modelling studies. To create the most beneficial conservation plan for areas of high suitability, a confident understanding of both the realized niche as well as the fundamental niche must be gained, using both current and historical data.

3.3.3.3 Overfitting

Overfitting of an ecological model occurs when the predictions of the model fits the initial inputted occurrence data too closely and therefore will fail to predict independent evaluation data accurately, which means failing to accurately predict suitable areas outside the current distribution (Radosavljevic and Anderson, 2014). This often occurs in models with little occurrence data and a large number of features. These lack a large enough dataset to establish the true niche-based output as random noise data, which arises from random chance in sampling, has a larger effect on the small dataset. This causes overfitting to noise (Anderson and Gonzalez Jr., 2011). The suitability models for both the Siberian tiger and Amur leopard fall under these categories as both have a very small occurrence dataset and therefore there is a possibility that the final model may suffer from overfitting. Maxent attempts to reduce overfit with the built-in regularization. This gives each variable that is included in the model a penalty. The strength of this penalty is determined by a parameter that is multiplied by the weight given to that variable in the model (Phillips *et al.,* 2006). Overfitting analysis can also attempt to overcome this caveat. Species tuning is one such method. This uses model evaluations that attempt to use occurrence data points from other geographic areas, rather than just those intermixed with those included in the model (Araújo and Rahbek, 2006). Although a valuable tool, this would not be applicable with the aims of this study. Both species exist in a very small distribution and so the inclusion of data from outside the study zone is impossible. Whilst there are other overfitting analysis tools, the unfortunate conservation status and distribution means that this it is highly unlikely that overfitting can be avoided and therefore thus may be the best possible option at this point.

3.3.4 Assessment of Identified Suitable Areas

The suggested areas of new habitat identified by this study all exist within the respective historic distributions of the Siberian tiger and the Amur leopard. While many of these habitats were occupied many years previous, the ecological variables that characterise these regions have changed hugely. It is obvious that the entire historic distributions of each predator species are no longer suitable for them, but the findings of this study give hope and direction for recovery in parts of them. Despite these positive findings there are a number of differences between my findings and others, which must be considered as part of the conservation process. The exact distribution of both predator species is not confidently known and therefore there is a possibility that these suggested locations could already contain Amur leopards and Siberian tigers, the lack of data for these areas in this study means that they will be considered as areas suitable for potential reintroductions even if they are actually already in use.

3.3.4.1 DPR Korea

The historic distribution of both the Amur leopard and the Siberian tiger includes the DPR Korea, but due to limitations inherent to various predictor variables, suitability models of the country have been absent. However, this region could still contain key areas for the conservation and future existence of both species. Hence, the inclusion of the DPR Korea in this study represents fundamental information for the protection and future status of the Amur leopard and Siberian tiger. The suggestion that there is as much as >9000 km^2 of suitable habitat for the Amur leopard and >6000 km^2 for the Siberian tiger in the DRC Korea, as identified by this study should be the focus of future research, with an investigation into localised prey movement and occurrence alongside the impact humans will have on these suggested areas for big carnivore conservation.

3.3.4.2 Amur Leopard Suitability Assessment

While the majority of the current Amur leopard population exists within the RFE, specifically the land of the leopard national park, this study suggests that it is the Jilin and Heilongjiang provinces of Manchuria that offer the largest quantity of suitable habitat outside of the current distribution. Much of these suggested areas occur as part of the Wanda Mountains, an area that was historically part of the Amur leopard distribution, but from which they disappeared in the 1980/90s (Yang *et al*., 2016). The seven areas within the Heilongjiang province (7 areas are entirely in this province while 2 further areas stretch across the border into Russia) largely mirror those found by other suitability studies for the leopard in north eastern China (e.g. Jiang *et al*., 2015). However, the areas located to the north and west of the Suiphun-Khanka meadows and forest meadows represent a larger collective area of potentially suitable habitat than suggested by previous studies (Fig. 11). While these 7 areas should not be considered independently, together, with the right conservation practices (discussed further in chapter 4), there is more than 6000km^2 of potentially suitable habitat here. Jiang *et al*. (2015) suggested 2 areas in this region, using the criteria of being more than 500km^2, while other smaller areas could be identified in this region, but these did not satisfy their set criteria. 4 of the areas suggested by this study fit with this criterion, hence representing an increase in area of which further research and consideration can be focused. The suggestion of this suitable habitat to the north of the flooded forest biome, identified by both this study and that of Jiang *et al*. (2015), prompts serious consideration of this region as containing future reintroduction and conservation priority areas. The single area I found within the Jilin provice of China, furthermore, was not identified by Jiang *et al*., (2015) however areas to the south were suggested in that paper. These areas were not identified as new sites here as they existed in areas where current occurrence data is present.

The potential for suitable habitat within the RFE appears limited (Fig. 12). A combined total of 384km^2, split into 2 areas (114 km^2 + 270 km^2), of suitable habitat. This potential area is located in the Ussurisky nature reserve, a region which has been previously discussed as an area of suitable habitat for future populations. Hebblewhite *et al*. (2011) identified 2451 km^2 of suitable habitat in this same area, while identifying a further 8197 km^2 across southern Primorskii Krai. The creation of this suitability model using both occurrence data from the RFE and China may be a cause for this variation in suitability. The level of human impact is considerably higher in north eastern China than in the RFE which may also contribute to a variation in ecological niche between the two countries. This could be especially relevant when considering that the majority of Amur leopard range in the RFE exists within the highly protected LLNP. The inclusion of localised prey occurrence by Hebblewhite *et al*., (2011) will have increased the sensitivity across this smaller area and is something on which further research should be focused in the areas put forth in this paper as suitable for reintroduction and as a priority for conservation.

a.) b.)

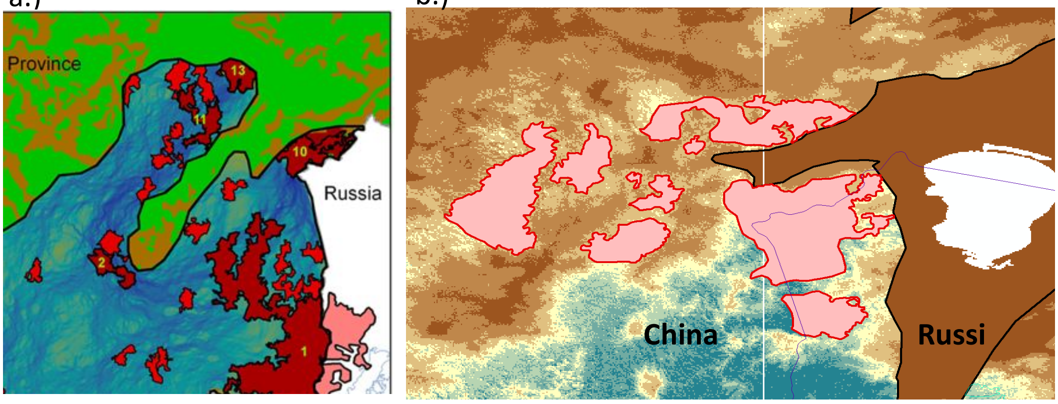

Figure 11. a.) Occurrence probability model for Amur leopard in north eastern China identified by Jiang et al. (2015). Red areas represent suitable patches with those with yellow numbers identifying patches >500km². b.) Suggested Amur leopard areas, from this study, within the Heilongjiang province of north east China. Demostrates the seperation of the areas by the Suiphun-Khanka meadows and forest meadows ecoregion.

a.) b.)

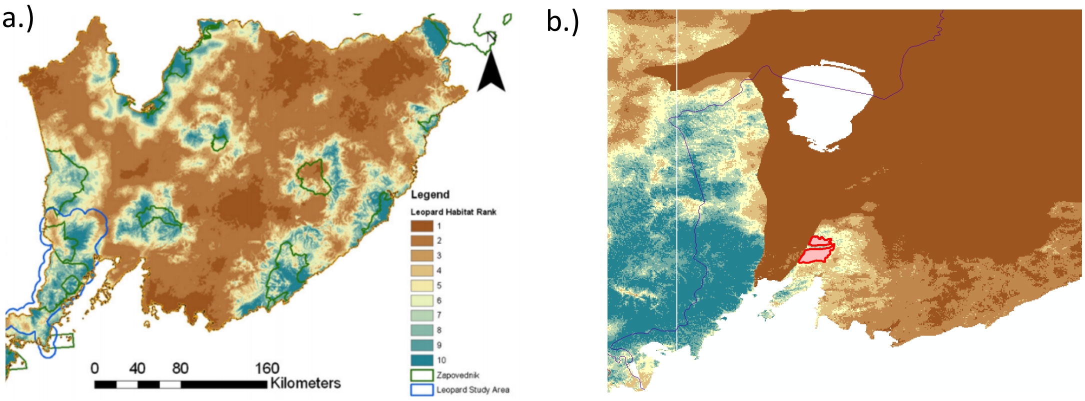

Figure 12. a.) Predicted Amur leopard habitat quality across their historic range in southern Primorksi Krai. Created using an all-prey species model (Hebblewhite et al., 2011). b.) Amur leopard suitability model with suggested areas within southern Primorski Krai, RFE.

3.3.4.3 Siberian Tiger Suitability Assessment

Despite once inhabiting much of the RFE, the Korean peninsula, north eastern China and stretching across to eastern Mongolia, the Siberian tiger now has its stronghold within the Sikhote-Alin Mountain range of Primorski Krai, RFE (Tian *et al*., 2011). The Krais to the north of Primorski Krai could represent a large area considered here as suitable for the tiger that could also act as a future stronghold (Fig. 13). Khabarovsk Krai and the Jewish Autonomous Oblast (JAO) were both inhabited by tigers, but they have been extirpated from both areas recently (Dou *et al.,* 2016). This region has not been discussed or considered as an area for tiger reintroductions. Instead, most conservationists have focused their efforts on Primorski Krai in Russia and provinces of northeastern China.

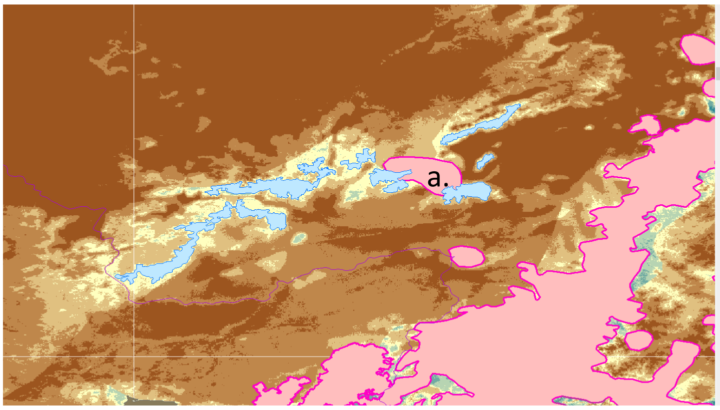

Figure 13. Suitability model for the Siberian tiger in Khabarovsk Krai and the JAO. The blue areas represent those suggested by the model. The pink represents the current range as suggested by the IUCN (Goodrich et al.*, 2015). a.) The IUCN current range area not being considered for this study.*

The IUCN describes a small area in this region as part of the current distribution (labelled a. in Fig. 13), but no data for this area could be found for use in the creation of my suitability model. This area's fragmentation from the rest of the described range also prompts uncertainty, with no obvious ecological corridor evident. While the suitability model suggests that this region could act as a future area for conservation priority, the requirement for a corridor for the Siberian tiger from this area to the current population must be established and maintained. Of the 4 large regions identified as especially suitable for tigers by my suitability model, it is this one which has the lowest human impact and the highest prey value. However, the region also has the lowest average suitability value. While the fundamental niche of the Siberian tiger may include this region, therefore, the current realized niche, which may have been heavily reduced by population and habitat loss, does not.

In parallel to other suitability investigations, the region along the Heilongjiang-Primorski Krai border represents the largest region that is considered to be highly suitability, with over 13900 km^2 (Fig. 14). The areas surrounding lake Khanka and along the western border of Primorski Krai were once considered to have some of the highest densities of Siberian tiger, but fragmentation and habitat degradation led to their extirpation (Hebblewhite *et al.,* 2014). While tiger presence is not recognised here by the IUCN current distribution map (Goodrich *et al.,* 2016), a tiger track survey in winter 2004/2005 found them to be present but very rare (Hebblewhite *et al.,* 2014). While human disturbance and anthropogenically-induced habitat degradation were found to be high in this region, Hebblewhite *et al.* (2014) identified areas that should be set aside for conservation priority in this region, this largely mirrors the findings in this study. The part of the region located on the Chinese side of the border discovered by my suitability model shows disparities to that of Xiaofeng *et al.* (2011), where this region was not distinguished as being of suitable quality for Siberian tigers. This region is however in agreement with the Mulin tiger conservation area (TCA) put forth by Hebblewhite *et al.,* (2012) which exists in an area of 3,231 km^2. With tigers having previously been present here, and the close proximity of this region to the current population within both the RFE and north east China, it is probably an important area for conservation priority. The part of the China-North Korea region on the Chinese side of the border was also identified by Hebblewhite *et al.,* (2012) as the Changbaishan TCA (North Korea was not included as part of this analysis).

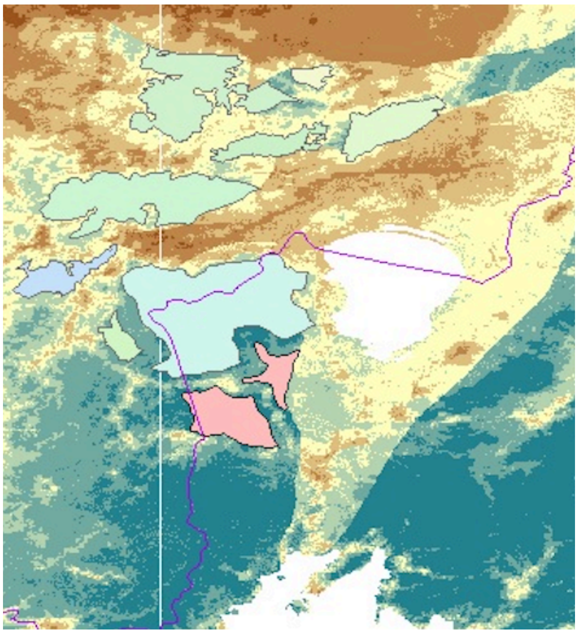

Figure 14. Suitability model showing the region of 10 areas across the Heilongjiang-Primorski Krai border

The fourth region, part of central Primorski Krai (Fig. 15), has few occurrence points found which are located on the edges of the suggested area. This would imply that the current absence of tigers is down to some factor not considered by the suitability models this area of apparent absence is surrounded by similar occupied territory. Of the 4 regions identified as important potential reintroduction sites, this contains the lowest suitability habitat, but conversely has very low human impact values. The study by Hebblewhite *et al.* (2014) found this region to be unsuitable for the Siberian tiger. A measure of habitat degradation was modelled as part of this study and stated this region as one which has suffered much from habitat degradation, while its higher elevation makes the occurrence of some prey species, like the Roe deer and Wapiti (considered a Red deer by the study), less likely.

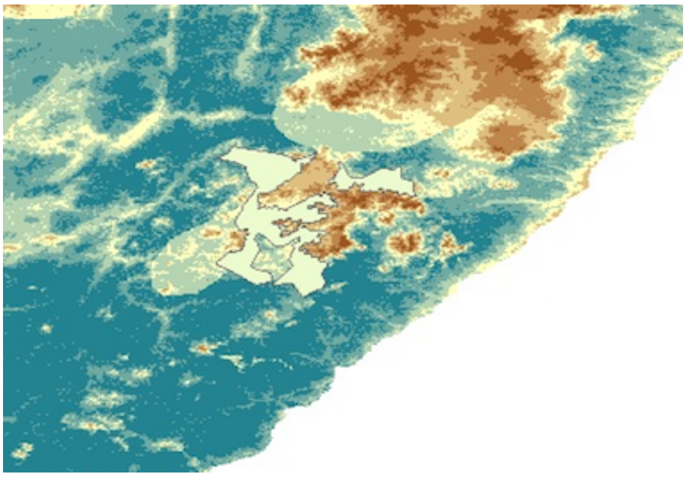

Figure 15. The region in central Primorski Krai, RFE. Surrounded by suitable habitat. The region is included in the Okhotsk-Manchurian taiga, part of the boreal forest biome, which is largely considered unsuitable for the Siberian tiger.

3.3.5 Assessment of Historical Distribution and Mechanics of Extinction

The entire historical distribution of both the Amur leopard and the Siberian tiger is no longer considered suitable, as found in this study. An increase in anthropogenic factors have driven these large carnivores out of what once would have been highly suitable ranges. This is particularly noticeable in north eastern China, where urbanization of the landscape and anthropogenic pressures have increased dramatically, forcing both predators back (Yang *et al.,* 2016; Miquelle *et al.,* 2010). Today, much of China is made up of large roads and cities with extremely few areas experiencing low or no anthropogenic pressures. Currently small populations of both Amur leopard and Siberian tiger persist in north eastern China within an existing reserve along the border with Primorski Krai (Xiaofeng *et al.,* 2011; Wang *et al.,* 2017). Other areas further from the border also offer suitable habitats, but, these small areas are not independently sufficient to support healthy populations. However, with the creation of corridors, these areas could offer cause for hope.

Historically, the Siberian tiger and Amur leopard existed in much larger areas within Primorski Krai. The suitability model from this study, alongside others, suggests a major constriction of suitable habitat within this region of the RFE (Hebblewhite *et al.,* 2014; Hebblewhite *et al.,* 2011; Stein *et al.,* 2016). The once primary forests of Primorski Krai have been transformed into secondary, broad leaf forests. This has been brought about by increasing anthropogenic perturbations (Tian *et al.,* 2011) while political uncertainty in Russia in the 1990s led many people exploiting the many resources of the surrounding forests (Miquelle *et al.,* 2010). This damaging of the forests has led to them now being unsuitable for sustainable populations of both predator species

3.3.6. Prioritizing of Tiger and Leopard Conservation Regions

3.3.6.1 Amur Leopard Areas and Regions

The suitability model for the Amur leopard identified 22,116km^2 of suitable habitat (Fig. 16 and Table 11), separated into 18 areas which can be further grouped into 4 regions (Table 12). Each of these 4 regions exist on the edge of the current distribution of the leopard and so offer potential for the expansion of future populations and an increase in Amur leopard numbers. The average anthropogenic impact will not give the true impact that humans will have on each area. The average impact upon a single location could be lowered if one particular type of impact is low, however, using the highest impact value will mean that the anthropogenic impact will always be considered, for example, if human density is considered high in a location but a road is not present, the impact of human density would be lower. Therefore, the modal value was selected. This is due to the edges of suggested areas being higher in human impact which will therefore raise the impact value, whereas the modal will show what the impact is across the entire area.

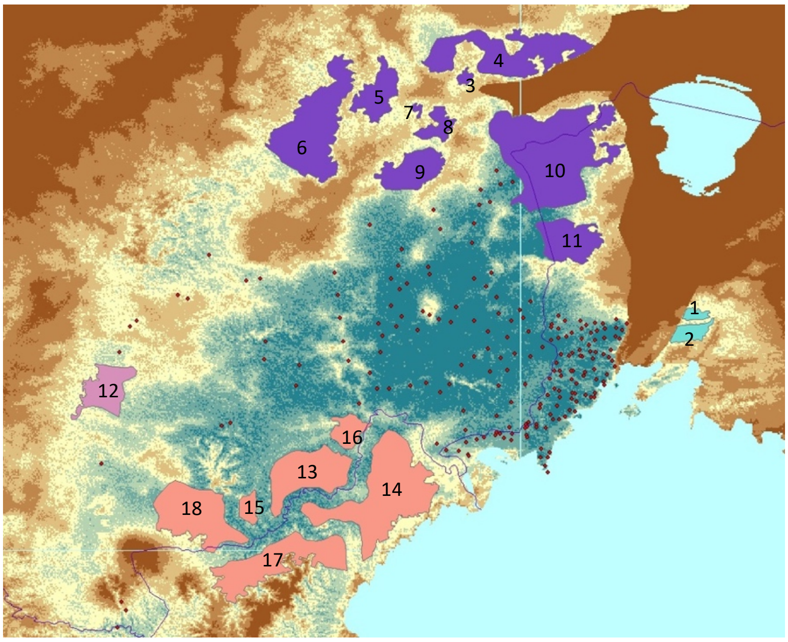

Figure 16. Suitability model for the Amur leopard showing the suggested areas with their respective numbers. Occurrence data locations are also shown. Blue represents areas of highest quality, dark brown represents poor quality with cream in the middle. Each of the four regions are displayed in a different colour. Region 1: Primoski Krai, is shown in light blue. Region 2: Primorski Krai-Heilongjiang, is shown in purple. Region 3: Jilin, is shown in lilac. Region 4: Jilin-DPR Korea, is shown in peach. Each area is also given a number for easier identification and referencing.

The 2 highest-scoring (most suitable) individual areas for the Amur leopard are part of region 4 in DPR Korea., This region also offers the highest average suitability. This region has not been heavily research as a potential Amur leopard habitat. The quality of information available, compared to that for other parts of the former and current distribution, has been lacking, but by using what data are available, some knowledge can be gained of the area and its potential. Yet, the suitability values still only come under the moderately suitable categorization (0.056-0.615) calculated from the threshold value and the average suitability of current locations. The 2 highest-scoring areas come close to this higher value but still remain below in. With over 9000km^2 of suitable habitat, the suitability model suggests that this may be a region that should be made a top conservation priority for the Amur leopard. Areas 13 and 16, which have the largest suitability values, could act as initial sites for release, while the remaining 4 would offer range for subsequent expansion. This differs from other suitability modelling for the Amur leopard, where regions of RFE and north eastern China have been suggested as offering the best habitat for the conservation and reintroduction of these big cats (Hebblewhite *et al.,* 204; Jiang *et al.,* 2015; Wang *et* *al.,* 2016), as this study is the first to suggest a region that exists within both the Jilin province of China and across the border into the DPR Korea. This could offer fundamental new information for the conservation of the Amur leopard.

*Table 11. Each of the suggested areas with their regions. 1.) Primorski Krai 2.) Primorski Krai-Heilongjiang 3.) Jilin 4.) Jilin-DPR Korea. The areas are given in descending order of their suitability value gathered from the model. The Human disturbance value is also given, gathered from the human disturbances model. The country letter after corresponds to the country in which the area lies (C – China, R – Russia, K – DPR Korea). *These areas stretch across a border therefore the letter represents the country in which most of the area exists.*

Area Number	Country	Size (km^2)	Region Number	Suitability Value	Human Value	Modal Human Value
13	C	1560	4	0.603	0.197	0.191
16	C	421	4	0.574	0.216	0.191
11*	R	1007	2	0.525	0.190	0.191
10*	R	4073	2	0.514	0.157	0.149
14	K	3186	4	0.495	0.189	0.191
15	C	230	4	0.487	0.174	0.148
18*	C	1844	4	0.467	0.178	0.149
17	K	1908	4	0.420	0.187	0.149
9	C	896	2	0.413	0.201	0.191
2	R	270	1	0.391	0.196	0.128
1	R	114	1	0.361	0.253	0.128
12	C	869	3	0.357	0.205	0.191
5	C	740	2	0.350	0.181	0.191
6	C	2437	2	0.340	0.205	0.191
7	C	45	2	0.336	0.196	0.149
4	C	2096	2	0.328	0.176	0.149
3	C	82	2	0.326	0.156	0.149
8	C	338	2	0.322	0.180	0.149

Table 12. Each of the four regions suggested for the Amur leopard with the size and the number of areas within each. The average suitability for the areas within the region is also given.

Region	Size (km^2)	Number of Areas Within	Average Suitability
1. Primorski Krai	384	2	0.376
2. Primorski Krai-Heilongjiang	11,714	9	0.384
3. Jilin	869	1	0.357
4. Jilin – DPR Korea	9,149	6	0.508
Total	22,116		

Areas 10 and 11, both predominately in Russia, are considered the 3rd and 4th most suitable areas respectively on the basis of suitability. Together these two areas make up 5800km^{2}of new habitat, and therefore offer great potential for new populations of Amur leopard. The further areas that are within the Heilongjiang province of China offer the lowest suitability of all suggested areas. However, as previously stated, this is based on the already limited current distribution of the leopard, and investigation into their true niche could raise the suitability of this area. Therefore, this region should not yet be discredited, and further research would give a better understanding of its potential.

Area 1, part of southern Primorski Krai, offers 384 km^2 of suitable habitat. While this region is not considered among the areas with the lowest suitability, its fragmentation from the current Amur leopard population and other suggested regions means that only a small population would be able to exist here, and gene flow would not naturally occur. This would make the population in this region unsustainable. If a corridor could be set up between this region and the current population, through the Suiphun-Khanka meadows and forest meadows, then the potential for a self-sustaining population is enhanced. Although not identified by their suitability model, Hebblewhite *et al.* (2011) suggested further regions, including this region, for Amur leopard reintroduction and therefore this region should not be ignored.

The final region, within the Jilin province of China, should act as an extension of the current population. While Amur leopard presence has occurred in the areas to the east of the suggested one, these reports are rare. With the increasing conservation actions in place, this region would add 869 km^2 of suitable habitat. This area does offer one of the highest average human impact values but when investigating the modal value, appears consistent with the other suggested areas. The largest problem that faces potential expansion of leopard habitat in north eastern China are the many large roads. This would require concerted action to reduce risk of collision, injury and deaths. This region would not seem to merit the status of an area of conservation priority yet, because of this problem. However, if the population currently in the Jilin region increases and can become stable then this area will offer a large increase in habitat.

This model suggests that the regions across the Jilin-DPR Korea border and Primorski Krai-Heilongjiang border should be classified as the top conservation priorities for the Amur leopard. Together they offer >20,000 km^2 of additional suitable habitat, while being in close proximity to the current population.

3.3.6.2 Siberian Tiger Areas and Regions

From the suitability model, 29,666km^2 of additional suitable habitat has been identified for the Siberian tiger within its historical distribution in far-eastern Asia (Fig. 17 and Table 13). The 25 suitable areas identified exist within 4 separate regions (Table 14). Each of these regions offer areas which could help meet the goals set by the Global Tiger Initiative (GTI) at the St. Petersburg Declaration 2010, and double the tiger population (Walston *et al*., 2010; Wikramanayake *et al*., 2010).

Of the suggested areas, the four with the highest average suitability all reside within region 2 (Fig. 17c. As stated earlier, Siberian tiger presence has been recorded in this area, albeit rare. According to the IUCN's geographic description of the tiger, however, this is not currently the case. While the possibility of tiger occurrence here is fairly strong, due to the high suitability value and the adjoining region of known tiger presence to the south, the confidence for stating presence appears to be lacking. Therefore, this region should be considered an area for conservation priority, either for the rediscovery of extant tigers already occupying it or as a potentially easy-access area for expansion of the adjacent populations.

The region across the DPR Korea and Jilin province border (Figure 17d), which is made up of six areas and stretches across 6101km^2, offers the areas with the next highest suitability. As stated with the Amur leopard, the DPR Korea has not been included in suitability models for the Siberian tiger and the availability of data has long been lacking, but this region does offer much promise for an increase in tiger population. This study presents some of the first research into the potential of DPR Korea as a future tiger stronghold and should be used as a starter for further and continued research into this region. This suggested region is in close contact with the current Siberian tiger population in the RFE and north eastern China and so movement and constant gene flow could easily be maintained here. Areas 21, 19 and 18 in particular are the areas with the highest suitability values in the region and would represent founder areas for the initial release of translocated or captive bred individuals. Areas 21 and 19 in the DPR Korea, a nation that is not part of CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) could be more problematic and this will be discussed further in chapter 4. The remaining 3 other areas offer suitable areas in which this initial population can grow and expand.

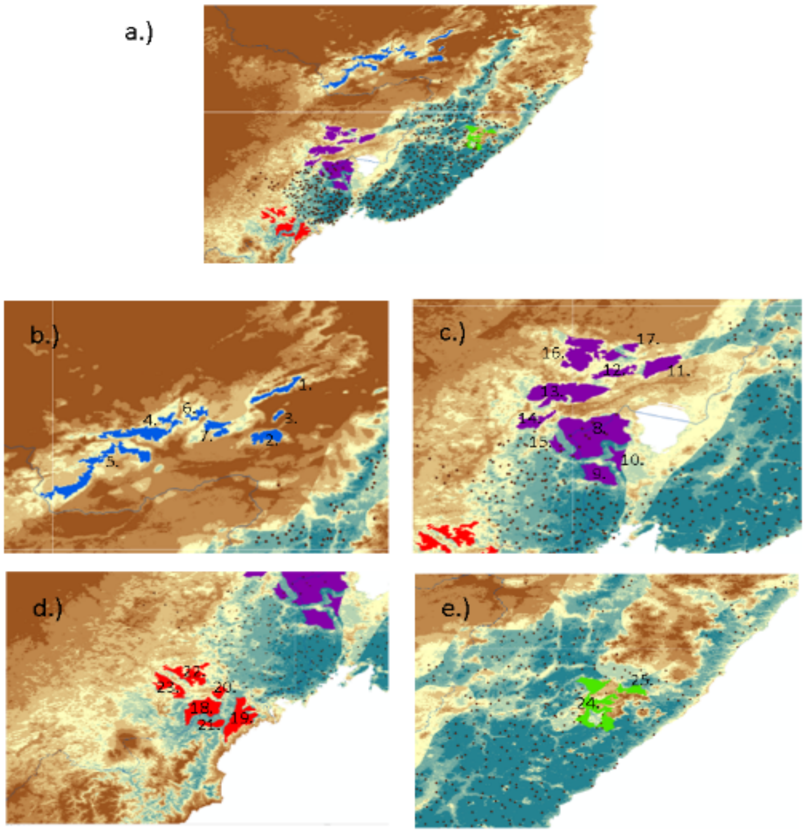

Figure 17. Suitability model for the Siberian tiger demonstrating the suggested areas with their respective numbers. Blue areas represent those of highest suitability, dark brown represents the lowest quality with cream in between. a.) Suitability across the entire study area. b.) Region 1 - Khabarovsk Krai and JAO. c.) Region 2 - Primorski Krai and Heilongjiang. d.) Region 3 -Jilin and DPR Korea. e.) Region 4 - Primorski Krai.

*Table 13. Each suggested Siberian tiger area in order of average suitability value. Each region in which the area exists, 1.) Khabarovsk Krai-JAO. 2.) Primorski Krai-Heilongjiang. 3.) Jilin-DPR Korea. 4.) Primorski Krai. The average human impact value is given (scale of 0-1, the lower value demonstrates a lower impact) as well as the modal value. The small letter after the area number corresponds to the country in which it lies if the region stretches across a border (c – China, r – Russia, K – DPR Korea). *These areas stretch across a border therefore the letter represents the country in which most of the area exists.*

Area Number	Size (km^2)	Region Number	Suitability Value	Human Impact Value	Modal Human Impact Value
9r*	1171	2	0.740	0.183	0.191
10r	461	2	0.694	0.157	0.106
8r*	4757	2	0.688	0.151	0.149
15c	306	2	0.658	0.169	0.149

21k	419	3	0.633	0.178	0.191
4r	1766	1	0.628	0.075	0.075
19k	1767	3	0.628	0.169	0.149
18r	1504	3	0.614	0.192	0.191
11c	1053	2	0.576	0.156	0.149
13c	2700	2	0.511	0.172	0.149
17c	204	2	0.510	0.150	0.149
20r	366	3	0.488	0.202	0.191
14c	678	2	0.479	0.163	0.149
12c	658	2	0.473	0.159	0.149
16c	1979	2	0.465	0.161	0.149
22c	1155	3	0.462	0.158	0.149
23c	890	3	0.450	0.162	0.149
24r	2522	4	0.436	0.043	0.054
1r	614	1	0.434	0.039	0.022
5r	2395	1	0.432	0.059	0.075
7r	645	1	0.417	0.041	0.032
25r	458	4	0.412	0.025	0.022
6r	307	1	0.407	0.054	0.032
2r	767	1	0.391	0.035	0.022
3r	124	1	0.346	0.036	0.022

Table 14. Each of the four regions suggested for the Siberian tiger with the size and the number of areas within each. The average suitability for the areas within the region is also given.

	Region	Size (km^2)	Number of Areas Within	Average Suitability
1.	**Khabarovsk Krai - JAO**	6618	7	0.437
2.	**Primorski Krai-Heilongjiang**	13,967	10	0.580
3.	**Jilin – DPR Korea**	6101	6	0.546
4.	**Primorski Krai**	2980	2	0.424
	Total	29,666		

The third region identified by the suitability model as a potential location for reintroductions lies to the north of the current population stronghold in Primorski Krai (Fig. 17b). Khabarovsk Krai once held healthy numbers of Siberian tigers but today a considerably smaller population exists, predominately along the border with Primorski Krai (Matyushkin *et al.*, 1996; Veselovsky, 1967). The JAO (Jewish Autonomous Oblast), neighbouring Khabarovsk Krai to the west, was also once a prevalent area for tigers. However, their residence in the JAO, and larger Amur region, ceased in the 1960s with no recorded populations since (Pikunov, 2014). This population in the JAO was suggested to have been genetically isolated and supplemented by individuals moving across the Chinese border from the mountain ranges in Manchuria, an area again where Siberian tigers are now rare, if present at all (Russello *et al*., 2004). As discussed in section 3.3.5, the data used for this model allows for only the current realized niche to be modelled and therefore, the suitability suggested for this region may be fundamentally lower than the true value if important variables and areas where tigers could live have been missed. The disappearance of Siberian tigers from much of these two constituent entities of Russia appears to be due to persistent hunting, civil war trouble and genetic isolation (Kucherenko, 2001). This suggests that it was not the unsuitability of habitat that led to their extirpation in this region and it therefore may still offer the suitable habitat that is required for the conservation of these cats. The human impact in these areas are considered the lowest of all regions and therefore the evidence suggests that the mechanics of the original extirpation may have ceased acting. While it must be stated that a low human impact may not be directly linked to reduced poaching, this still counts among the initial, positive evidence for potential reintroductions into this region. The distance of this region from current populations would then persist as the key issue for conservationists (this will be further discussed in chapter 4). While this region should not currently be considered as a conservation priority area, it should be the focus of much future research into its potential for future populations, using investigations of ecological niche dynamics and human attitudes in the region.

Areas 24 and 25 were also identified by the suitability model as a region of suitability for the Siberian tiger (Fig. 17e). This region lies in the southern part of the Okhotsk-Manchurian taiga, a biome that is mostly considered unsuitable by the model. The values for anthropogenic impact are also low for this region. The lack of any barrier to dispersal obvious from the model suggests that a further factor (as yet unknown) is preventing the tiger from expanding into the region as it does not appear isolated. With almost 3000km^2 of suggested suitable habitat here, this region could offer habitat for numerous individuals. However, at present, I cannot recommend this region for conservation priority before local scale research has not been conducted to identify the factor that is currently preventing tiger occurrence in this region. This research could also offer a useful critical analysis of this suitability model's findings and suggest further variables for inclusion in future models that were absent here.

3.3.7 Final Conservation Prioritizing Assessment with Competition

3.3.7.1 Competition Assessment

Like many other sympatric large predators, the Siberian tiger and Amur leopard coexist through various means of avoidance and partitioning. In Nepal competition between leopards and tigers is avoided via direct spatial avoidance (Carter *et al.,* 2015) while in southern India competition was minimised through ecological separation. In this region, the activity patterns of prey determine the activity of their respective predators, and this distinctive activity pattern reduces the encounter rate between the two cats (Karanth and Sunquist, 2000). However, it is highly likely that it is a combination of these factors and other ecological actions that contribute towards the overall reduction of potential niche overlap and competition between the two species.

In the forests of the RFE and north-eastern China, a dietary overlap exists between the two predators (Yang *et al.,* 2018). Therefore, spatial displacement may act as a more beneficial method to avoid conflict. Amur leopards are seen to frequent ridge trails whereas Siberian tigers will travel using lower altitude, riverine valleys. A difference in activity behaviour has also been attributed with leopards predominately diurnal and tigers more nocturnal (Wang *et al.,* 2017). However, compared to other ecosystems where these two predators are sympatric, the lower availability of prey increases the likelihood of conflict. During these conflicts, the much smaller leopard is often killed. This results in an inverse relationship between leopard and tiger density (Jiang *et al.,* 2015). Intraguild competition is little discussed in conservation programmes for predators (Jiang *et al.,* 2015). For a species as rare and threatened as the Amur leopard, this must be considered alongside habitat suitability and human impacts to maximise the potential for reintroduced populations to become self-sustaining and, consequentially, increase. To explore this factor in this study, each area and region found to be suitable for Amur leopards and Siberian tigers respectively will be ranked, taking into account the suitability value and anthropogenic impact.

Areas and regions which represent suitable habitat for both predators will then be considered in detail to determine to which of the two species the area has the highest potential value.

The two conservation priority regions suggested for the Amur leopard (Fig. 10), Primorski Krai-Heilongjiang and Jilin-DPR Korea, are also highly suitable and hence suggested for the Siberian tiger (Fig. 11). Both offer a potentially large increase in the range of the species into suitable habitat. Therefore, prioritizing of each region will maximise the potential for successful conservation programmes, avoiding the Intraguild competition that has inhibited the Amur leopard previously.

3.3.7.2 Jilin-DPR Korea Region

Little evidence exists, within the literature, of the presence of either Siberian tiger or Amur leopard within the Korean peninsula, despite being part of the former range of both species (Jiang *et al.,* 2015; Dou *et al.,* 2016). Part of this historic range is suggested, by my suitability model, as a conservation priority for each species. The suggested region that might be important to both taxa borders the current populations of tiger and leopard in southern Primorski Krai and the Jilin province of China (see Fig. 10, region 4, and Fig. 11d). Both species could benefit from this increase in range. This region was, however, ranked as the most suitable for the Amur leopard, while it was ranked second for the Siberian tiger. This region is therefore selected as a conservation priority for the Amur leopard and consequently will not be suggested for the Siberian tiger at this time.

The 9,149 km^2 of new range offers a 75% increase of range for the Amur leopard (21,355 km^2), which could vastly increase the critically low population currently seen. Despite not being the largest, this region is considered to have the highest suitability value, while areas 13 and 16 are considered the best of all the areas identified across the entire study. Keeping this area solely for the leopard will avoid the intraguild competition between the species and hence, offer a higher chance of success in Amur leopard conservation.

3.3.7.3 Primorski Krai-Heilongjiang Region

Primorski Krai is a stronghold for both the Amur leopard and the Siberian tiger, with majority of each species' population already residing within the region (WWF, 2012; Wang *et al.,* 2016). The remaining population of leopard is situated in the most southernly part of Primorski Krai, in the LLNP, whereas the tiger has populations spreading further north towards the border and into the neighbouring Khabarovsk Krai. Despite being suggested as one of the two most suitable regions for the reintroduction of each species, this region should be designated as a conservation priority for the Siberian tiger rather than the leopard.

This region offers 13,967 km^2 of new habitat for the Siberian tiger, this will increase the range to 109,697 km^2 (a 15% increase). This is the region with the highest average suitability for the tiger while also being the largest new block of habitat found for this species. All four of the areas with the highest suitability for tigers exist within this region.

3.3.8 Summary

Despite large areas and regions being initially suggested by the suitability model as potential reintroduction sites for the Siberian tiger and the Amur leopard, analysis of each block's connectivity and other factors like intraguild competition offers more insight and suggests a more nuanced view. The location of each region and area in respect to the current populations along with the potential for intraguild competition, which negatively impacts the smaller Amur leopard particularly, limits the potential of some regions were we to reintroduce both taxa. I have therefore suggested that region 2, Primorski Krai-Heilongjiang, be prioritised for the Amur leopard and region 3, Jilin-DPR Korea, for the Siberian tiger.

The inclusion of the Korean peninsula in my model is a first in suitability modelling for these species and its inclusion has revealed a large region which could be considered as a conservation priority for the Amur leopard. It also offers high suitability for the Siberian tiger but is not suggested as the avoidance of interspecific competition is wanted to best aid in a successful conservation plan for the critically endangered Amur leopard. A large region within Primorski Krai and Heilongjiang is classified as a conservation priority for the Siberian tiger, with this region offering the highest suitability discovered by the model. A further region within Khabarovsk Krai and the JAO is suggested for the Siberian tiger but not considered as a conservation priority. This region has a low suitability, however it was once an area where tiger density was high. It will therefore be included in the consideration of further conservation actions in chapter 4. This will be to analyse its potential and the actions that must be put into place to realise it. Further investigations into the region's suitability and the fundamental vs realised niche of the Siberian tiger should be conducted to estimate the exact suitability and potential for this region in future programmes.

While this study does offer suggestions, it is not proposing a final conservation plan for the Amur leopard and Siberian tiger. Further research is vital and therefore this study, and the model created, should be seen as offering new knowledge and the potential to benefit and shape conservation plans for these extremely rare and threatened species.

Chapter Four: Proposed Conservation Actions for the Siberian Tiger and Amur Leopard

4.1 Introduction

Suitability models for the Siberian tiger and Amur leopard, created using various biotic and abiotic variables, revealed a single region for each species that is likely to be particularly important for their conservation. While these regions may offer hope for future reintroduction programmes, much additional work and increased knowledge of conservationists and local people must occur before any programme is designed and put into practice. Although the data used were of the highest quality available, higher quality still should be useful for future work. Constant monitoring of environmental variables, as well as further analyses designed to identify additional variables that may have effects, even minimal, on big cats in this region will only improve suitability models and expand on findings within this study and others.

For reintroduction programmes to be successful, both in situ and ex situ practical work is required. Suitability models incorporate the available scientific knowledge while work in situ, working with big cat habitats, infrastructures and local people, will give an understanding of the potential and likelihood of an effective programme. Ex situ conservation, through breeding programmes, will help to increase the gene pool and potentially provide individuals for future release. Both are required, in considerable quantity, for a successful programme to be established.

This final section will discuss conservation actions that could or should be considered for these species on the basis of the work presented in Chapters 2-3, to point the way for this future work. For instance, here I consider the requirement for ecological corridors in zones where reintroductions have been suggested. Without these, suggested areas of suitable habitat for these cats are fragmented both from each other but also from the current populations. For a healthy and sustainable population, these areas must all be linked. These areas will also require monitoring with possible anthropogenic sanctions to prevent the continuation of historical extirpation of each species from these areas. This chapter will also discuss gap analysis (a method comparing a species distribution with the distribution of different land management classifications (Scott *et al.,* 1993)), biosocial conservation (a relatively new branch of conservation science that is at the forefront of any reintroduction programme particularly for large predators), and the guidelines put forth by the IUCN and in previous reintroduction programmes will be discussed. The chapter aims to establish the next steps in the development of conservation plans for the Siberian tiger and Amur leopard.

4.2 Ecological Corridors

4.2.1 Introduction

Having established the potential carrying capacities of the areas identified in Chapter 3 as key conservation zones for the Siberian tiger and Amur leopard, the conservation community will need to consider their connectivity. As previously discussed in chapter 1 (1.10), ecological corridors are fundamental to conservation. Fragmentation of habitat can prove detrimental to a species and its ecological community, as it creates dispersal barriers (Debinski and Holt, 2000). This can lead to low population densities, where the species is at a higher risk to extirpation, and a lack of immigration prevents a bolstering of the population. A number of other problems can also arise from fragmentation; populations can become habitat specialists; the chance of equal male/female offspring will reduce, and genetic bottlenecks can occur. All of these can prove additionally damaging (Bright, 1993).

The installation of corridors between isolated populations can help prevent all of these negative effects. Immigration and emigration can be allowed, increasing the gene pool of the connected populations and attaining sustainability where isolated sub-populations would experience much higher risks (Bennett, 1990; Lees and Peres, 2008). The carrying capacity estimates I have presented (section 4.2 above) depend on the installation of corridors between separate areas within each region, as some of the suggested areas are only able to sustain a small population of tigers and would be considered unviable if isolated. Linking these areas to one another and to the current population would enable the installation of these regions as conservation priority zones and make them suitable for reintroduction.

The potential for ecological corridors for the Siberian tiger and Amur leopard has been the focus of previous studies. One such investigated the potential for corridors within the region of the Razdolnaya river basin, an area that is currently limiting the movement of both species (Miquelle *et al.,* 2015). In this region, a potential corridor, that would serve as a gateway between southwest Primorski Krai and the southern region of the Sikhote-Alin mountains, was found with much of it falling within forested areas. However, a major highway still poses a substantial problem for this corridor. Miquelle *et al.* (2015) has suggested the use of over or underpasses to aid and allow the free movement of both tigers and the leopard, along with other animal species. As part of the current work being conducted in both Northeastern China and the Russian Far East, corridors between areas with populations of both species have been discussed, suggested and further investigated to assess their viability. One such discussed corridor is located in Dapanling, in the basin of the Tumen river. As part of this discussion it was stated that an underground passageway was required, to avoid roads, and protection laws for the vegetation, ensuring that the habitat remains (HFA and WCS, 2000).

For this study, I created a corridor model which help to validate regions as suitable for reintroduced populations and hence, the long-term conservation of the Amur leopard and Siberian tiger.

4.2.2 Suggested Ecological Corridors

Investigation of potential paths between the suggested reintroduction regions and current populations is vital for a healthy and sustainable population (Haddad *et al.,* 2003). Least-cost path analysis is a technique that has been used in previous conservation studies for big cats (Hebblewhite *et al.,* 2011). It models the relative cost for a species to travel between two set areas (LaRue and Nielsen, 2008; Carroll and Miquelle, 2006). The expert least-cost analysis can be based on the suitability model, where areas of high suitability are considered the lowest cost to transverse with the shortest distance between the two areas then selected. The model can then be displayed, highlighting areas above the threshold, between it and lowest variable not considered an outlier, and below this lowest variable. Cost values below the threshold value will be completely avoided while values below the lowest variable not considered an outlier will be avoided where possible. From the expert least-cost path analysis, linkages can be modelled suggesting the best avenue for an ecological corridor, based purely on the suitability model.

The expert least-cost path analysis created using ArcMap 10.5.1, for the Amur leopard revealed possibilities for the construction of ecological corridors within the region, and between the suggested areas and the current population (Fig. 18). Two regions were considered for the Siberian tiger, the region in Primorski Krai-Heilongjiang suggested as a current conservation priority, and the region in Khabarovsk Krai and the JAO that is suggested for future conservation work (Fig 19.). Expert least cost path analysis for the region suggested for future conservation work shows that much of the region would have a high cost for movement of the Siberian tiger, based on the suitability model outputs from Chapter 3.

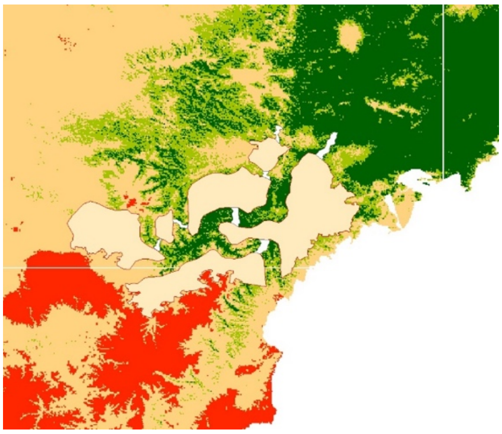

Figure 18. Expert least-cost analysis for the Amur leopard within the suggest region in DPR Korea- Jilin. Dark green represents areas of lowest cost for movement, cream represents a cost between the threshold and lowest variable not considered an outlier, and red represents the highest cost, below the threshold value. Areas in green represent areas with the least-cost and hence best options for corridors. The linkages are displayed in white and represent the corridor considered to be through the areas of least cost, while also being the closest point between each respective area.

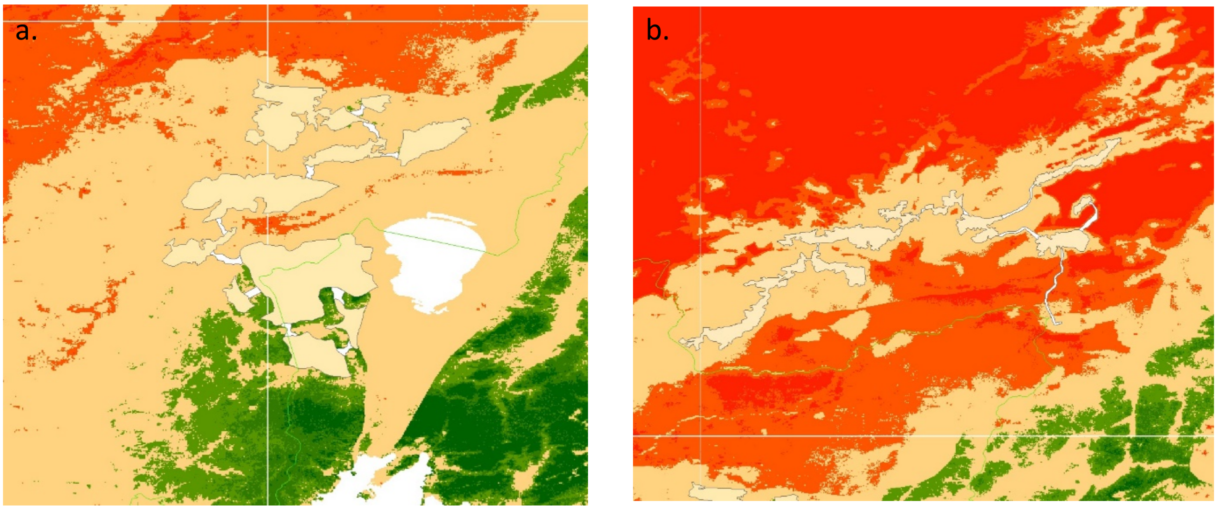

Figure 19. Expert least-cost path analysis with linkages for the Siberian tiger in the suggested region within a.) Primorski Krai and the Heilongjiang province of China and b.) Khabarovsk Krai and the JAO. Red areas represent those areas below the threshold value, with the areas in cream representing values between the threshold and the lowest variable not considered an outlier. Areas in green represent areas with the least-cost and hence best options for corridors. The linkages are displayed in white.

While these linkages represent the shortest distance and least cost between each respective area, this may not represent the best option for an ecological corridor. Localised analysis of the road network may identify areas of road that will serve as the best location for an ecological bridge, or some other method of crossing the road. Other barriers, not identified by the suitability or human disturbances model, may also prevent the creation of these corridors, underlining the need for further localised monitoring and conservation work.

4.3 Gap Analysis

Gap analysis allows for the results of a suitability model to be compared with existing reserves, so that gaps in protective networks for biodiversity can be identified (Scott *et al.,* 1993). These gaps can then be focus for the creation of new, preferably strictly controlled, reserves which best target the focal species. These reserves then represent among the best available habitat with minimal anthropogenic interference, allowing the species to exist without risk of poaching or other human induced mortalities. These strictly protected reserves have benefited both the Siberian tiger and especially the Amur leopard in the LLNP.

The creation of the 262,000 hectare LLNP in 2012 grouped together three previous parks along with a stretch of land along the Chinese border that included 60% of the existing Amur leopard's global population. The strict protection established in the park had enabled the population of Amur leopard to steadily rise, with individuals then spreading into the neighbouring provinces of Heilongjiang and Jilin in north east China (WWF, 2012). Nature reserves within China, along the border with Primorski Krai, have also been set up to protect a large, continuous section of leopard the leopard (Wang *et al.,* 2017). This demonstrates the effect that a protected region has already had on the species. However, these protected areas still only represent a relatively small range for the species and the inbreeding crisis now being seen in the species is continuing (Hebblewhite *et al.,* 2011). A further protected reserve has been suggested and investigated in the Heilongjiang region of China, areas where the Siberian tiger is already present. This reserve would be linked to Pogranichny Raion in Russia and would therefore stretch across the border offering more protection (HFA and WCS, 2000). Forested regions in part of the RFE have been leased to NGOs as part of a "nature-protection" concession, with the purpose of protecting and preserving these rare habitats. A 25 year lease was taken out by an NGO for a forested region of 45,000 hectares. This region had previously suffered much devastation as a result of fires but this new protection will allow for the full recovery of the ecosystem (Aramilev *et al.,* 2014).

Whilst much land has been given or is being considered for necessary protection (Fig. 20), much of the suggested regions do not exist within these zones. The two regions suggested as conservation priorities in this study both include some areas within established nature reserves or national parks, but most of their land falls in areas where strict rules are absent and reintroduced predators would face many of the problems that resulted in their original extirpation from the area (Xiaofeng *et al.,* 2011). Therefore, the creation of a single, large protected region, as done with the LLNP, would be of biggest benefit, so that large scale monitoring and protection can be maintained over the entire region with the reinforcement of uniform, strict protection requirements. Failing this, next stages for the reintroduction of the Siberian tiger and Amur leopard into the suggested regions should focus on making the areas outside of the protected nature reserves and national parks into safe areas where the species are not threatened by humans.

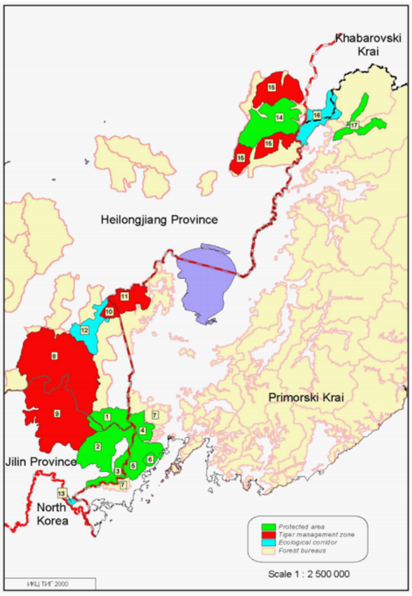

Figure 20. Map showing the proposed system of protected areas and tiger management zones around the current Siberian tiger population, as proposed by Miquelle et al., 2001)

4.4 Biosocial Conservation with Local Communities

4.4.1 Introduction to Biosocial Conservation

The conservation of biodiversity has always been a difficult problem, with no definitive formulation and no right or wrong methods (Setchell *et al.,* 2016). Gaining an understanding of the needs for each conservation action requires a community from different fields, including biological and social scientists, who work as a team to integrate the different ideas and practices (Green *et al.,* 2015). This has led to many conservation studies understanding that ecological knowledge alone is not enough (Fox *et al.,* 2006) and social and cultural aspects must be considered and respected, with this being referred to as 'Biosocial Conservation' (Setchell *et al.,* 2016).

It is now widely recognised that the threats that many of the world's species face are mainly anthropogenic (Ceballos *et al.,* 2015), so conservation efforts should be as much about the local people as they are about the target species/ecosystem (Setchell *et al.,* 2016). In the past projects have failed because conservationists and local people have clashed as a result of human welfare being disregarded (Chan *et al.,* 2007). For a full understanding of the different issues that can affect a conservation plan, anthropology, biology, development studies, geography, politics, psychology, education, economics and history are all areas that should be considered and represented on the conservation team (Newing, 2010; Setchell *et al.,* 2016). Integration of these social aspects into conservation efforts is now being actively promoted by nongovernmental and governmental organizations along with academics (Fox *et al.,* 2006). With each project, there will be both winners and losers and these must be identified, so that the responses can be predicted and appropriately dealt with (Chan *et al.,* 2007). Otherwise, the effective conservation of the target animals, plants and ecosystems may not be possible.

4.4.2 Maasai Lion Guardians

Conservation efforts for the lion (*Panthera leo*) in Southern Kenya are an example where local people and their cultures have been included in conservation planning resulting in a huge local success (Hazzah *et al.,* 2014). The local Maasai people have historically lived as pastoralists, rearing large herds of cattle. This has continuously brought them into contact with the lion (Hazzah, 2007). Retaliatory killings were, and in some regions still are, common after the loss of livestock, and there is a historic practice within Maasai culture of lion hunting as a rite of passage for young men (Goldman *et al.,* 2013).

Across Africa, lion populations have fallen severely and many projects in Kenya state that Maasai lion hunting is threatening the species with extinction (Hazzah *et al.,* 2009). With this information, conservationists began to draw upon local culture and knowledge to develop plans to aid the falling lion populations. The Lion Guardian programme was initiated where local Maasai were educated about decreasing lion numbers and provided with incentives to participate in the form of paid employment, literacy and scientific training, and community assistance (Hazzah *et al.,* 2014). The lion guardians directly monitor lion populations and movements as well as employing traditional Maasai conflict mitigation techniques that reduce the risk of livestock being taken (Dolrenry, 2013). This programme was widely used alongside a compensation programme where farmers who lose livestock to lion predation were given compensation payments. A combination of these two programmes in South Kenya led to a 99% drop in lion killing aiding hugely in lion conservation (Hazzah *et al.,* 2014). This led to conclusions stating that human involvement to promote human-carnivore coexistence represents one of the best methods for conservation of large predators.

4.4.3 Compensation Programmes

Compensation programmes have also been used in areas where other large carnivores coexist with humans. In a small region of Northern India and Mongolia, for instance, compensation was given to farmers who lost livestock to the snow leopard (*Panthera uncia*) (Mishra *et al.,* 2003). Although this was successful in reducing retaliatory killings, it was only in a relatively small area and to be considered a true success the spatial coverage of the programme should increase enormously (ibid.). Compensation is also given to farmers within the Khasan region of the Russian Far East when deer are lost to Amur leopard predation (Wang *et al.,* 2015). Compensation programmes have been a heavy part of conservation plans for the Siberian tiger and Amur leopard and have been put into operation in areas surrounding farms, however this has not been introduced across the entire range of both species (HFA and WCS, 2000).

4.4.4 Conclusion

Any conservation programme, especially for large mammalian predators who instil a historic fear in people, should place a clear focus on local people. Although there cannot be one single answer for all species, previous successful cases can be used as a basis for developing plans. The success of the Maasai lion guardians, for instance, can be used to aid in Siberian tiger and Amur leopard conservation. Talking to groups of local people, both those who have historically hunted these species and those who have not, can provide a better understanding of the consequences that the loss of a top order predator could have upon their local environment. The inclusion of these local people, offering the potential for jobs, will give incentives to protect these big cats that may start to replace the fear that has historically been associated with these species. The (already successful) use of compensation programmes can also be implemented further, across their entire range and also into these new suggested regions. To best understand the way that the biosocial conservation of these two species should be directed, frequent conversations with local governments, but more importantly, local people, will help to understand their thoughts and from this. "Public education of Siberian tiger conservation" has been installed in some preschools, primary and middle schools in northeastern China, educating children on the importance of the large predators in their forests (HFA and WCS, 2000). The extension of this into all parts of the RFE, the Korean peninsula and around the new suggested regions would further aid in the establishment and safety for the potential populations. This work cannot be done here but would be important to the implementation of the reintroductions I have suggested, especially given that the areas identified as suitable lie within the cats' historic ranges.

4.5 Criteria Suggested for the Reintroductions of a Species

4.5.1 Introduction

The reintroduction of a species should be deemed a last resort and only considered after the failure of previous conservation strategies (Hayward and Somers, 2009_b). Large mammalian predators are amongst the most reintroduced of all species (Seddon *et al.,* 2005). This may be largely attributed to the impact they can have on their respective ecosystems, as these taxa often act as keystone species or as a proxy for the health of their ecosystems (Seddon *et al.,* 2005; Sinclair *et al.,* 2003). The manner in which a reintroduction programme can be deemed a success is also highly debated, as the desired outcome should be confidently understood prior to the initial stages of the programme but is not always stated explicitly.

From prior studies, a population of >500 individuals of a species are deemed to be self-sustaining and therefore constitute a successful reintroduction (Griffith *et al.,* 1989). However, populations of large predators of this size are extremely rare and therefore many natural populations would be considered unsuccessful, had they stemmed from reintroduction programmes (Hayward and Somers, 2009_b).

For the Amur leopard reintroduction is thought to be the best hope of survival as populations and the gene pool are currently too small and have insufficient power to recover naturally (Hebblewhite *et al.,* 2011). The creation of a second population of leopards seems to be a necessity (WCS, 2001). Siberian tiger populations are not at the same drastically low levels of the Amur leopard, however populations are still considered critically low and the establishment of new populations in strictly protected areas is needed. Tiger Conservation Landscapes (TCLs) have been the focus of many ecological modelling studies (Wikramanayake *et al.,* 2011) for all tiger subspecies. They involve the establishment of protected conservation areas where tiger populations can recover. The landscapes are chosen where tiger presence has been observed in the previous 10 years and they are described as 'potential effective habitat' (Wikramanayake *et al.,* 2011). Alongside these, there have been suggestions for restoration landscape, an area where the tiger and other species are protected, which would help to solidify tiger populations (Sanderson *et al.,* 2010). Once we have confirmation or denial of Siberian tiger presence in the Heilongjiang-DPR Korea region, this region could act as either a TCL or as a restoration landscape.

4.5.2 Criteria Suggested within the Literature

Various studies have presented different criteria which can be used as a template for this study. Christie (2009) made suggestions regarding release site selection for the Amur leopard. Their selected release site was aimed towards the establishment of a secondary population, rather than supplementing the existing one. The target was to increase genetic representation in the population and the size of the gene pool. Christie's (2009) suggestions (Fig. 21) were made based on their scientific understanding of Amur leopard biology and general reintroduction science. Using each of the criteria put forth by Christie's (2009), the results and suggestions from this study can be tested, ensuring they match up with these criteria.

1. The historical range was the initial study area for the creation of my model.

2. The suggested region is not separated from the leopard's current range, however a fragmentation barrier, a major road, exists between. The suggestion of installing corridors, which include methods of road crossing could be excluded for this reintroduction. This would enable the new population to grow before allowing the mixing of the two populations.

3 and 4. Human habitation, along with overall impact and presence, and an abundance of prey was identified as the initial driving factors for my models.

5. The presence of cliffs and rocky areas were not included directly, however the inclusion of altitude, slope and aspect acts as a proxy for this, with areas of preferential conditions identified by MaxEnt during model creation.

6. Adequate infrastructure for the management of the reintroduced leopards is a necessity. Roads have often been associated with poaching (Haines *et al.,* 2012) and hence, large roads were actively avoided when selecting areas for potential reintroductions. The installation of small roads, not for public use, would be required in this new region. The creation of these would allow for the entirety of the region to be monitored, whilst also allowing protection services and scientists access to the more remote parts.

7. The final criterion is the aim of this conservation actions discussion. The implementation or further discussions of these points, focusing directly on the Amur leopard and Siberian tiger whilst also using previous successful reintroductions of other species, will help to make this suggested region well-managed with sufficient protection for the species to thrive.

Whilst these criteria were designed for the Amur leopard, they can also be used as a proxy for the Siberian tiger and their suggested reintroduction region. The creation of a new population separated from the current one is not required for the Siberian tiger and so can be ignored. Tigers do not require access to cliffs and rocky areas like Amur leopards do and instead are known to select riverine valleys. As for the leopard, the area identified can be assumed to already tackle these needs from the inclusion of topographical variables in the model.

1. *Be within the historical range of the Amur leopard.*
2. *Be sufficiently separated from the current range to ensure no possibility of genetic mixing with the existing population.*
3. *Be as far away as possible from human habitation in order to minimize chances of conflict.*
4. *Contain a high prey base of appropriate species.*
5. *Contain cliffs and rocky areas to facilitate the leopard's use of refuges on release.*
6. *Contain adequate infrastructure (roads, electricity and water supply) for management and monitoring activities.*
7. *Be within a well-managed area with sufficient protection.*

Figure 21. Criteria suggested by Christie (2009) for release site selection of a secondary population of the Amur leopard, with the aim of increasing the gene pool.

4.5.3 IUCN – Guidelines for Reintroductions

Various conservation strategies can be used when attempting to reinforce the population of a species. The IUCN and Big Cat Species Specialist Group have designed guidelines that will enable the correct conservation translocation to be selected, for the desired outcome, whilst putting forth criteria that should be met for the programme to continue (Fig. 22). Under these guidelines, both the Amur leopard and

Siberian tiger would fall into the group for which there is a requirement for population restoration through reintroduction.

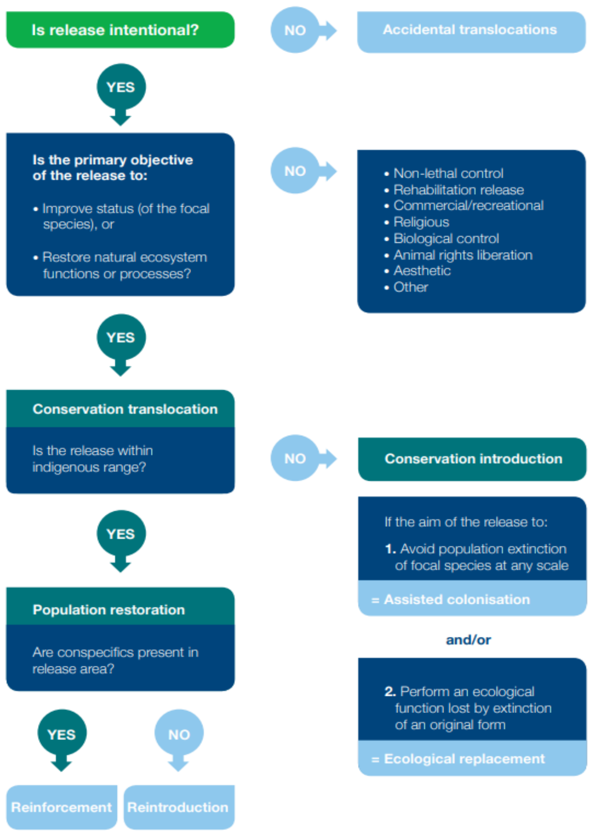

Figure 22. The translocation spectrum as designed and put forth by the IUCN. The typology of various conservation translocations. (IUCN/SSC, 2013).

For any translocation programme to be considered, we must first consider whether it is an acceptable option. Although a conservation programme may be the best, or possibly only, option for a species, the practicality or chances of success may suggest it is still not worthwhile. Many ecological, social and economic factors must be considered (IUCN/SSC, 2013). The regions that have been selected for reintroduction to take place, must have the factors behind the species' original extirpation removed or reduced to a sufficient extent. With both the Amur leopard and Siberian tiger older local extinctions are due to anthropogenic pressure and influence. In the regions suggested for reintroduction, anthropogenic presence and impact still exist to various extents. The prevention of these impacts, in the regions selected, will be crucial for any programme to be considered successful. Any reintroduction programme must thus be done concurrently with the establishment of nature reserves or natural parks with strict protection, where human presence is kept minimal.

Planning of the translocation must also include initial goals and objectives (Fig. 23). These should be very clear and the steps that are required to reach the goal should be stated. Goals are envisioned as statements that the conservation benefit of each action, including potential population increases (IUCN/SSC, 2013). For the Amur leopard and the Siberian tiger, establishment of new populations in regions considered to be of high suitability, with a high prey base, low anthropogenic impact and avoidance of competition between the species is the obvious goal. Along with these goals, a management and monitoring plan must be established. These monitoring programmes will need to state what will be used as a measurement of success; the data that should be collected to achieve this success and where and when it should be gathered; who will gather this data; and who will distribute the data to the appropriate people (IUCN/SSC, 2013). These are all questions that are a necessity for the future of the programme.

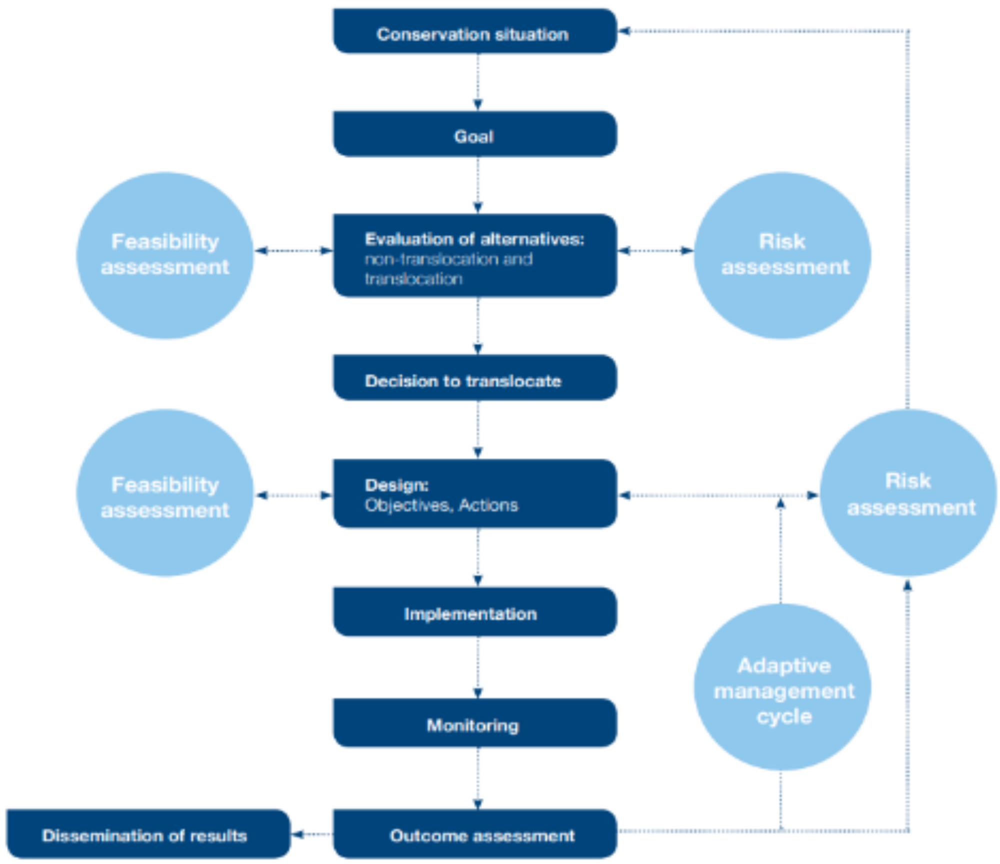

Figure 23. The conservation translocation cycle. Development of progress reviews through all stages of the reintroduction and aid in reaching the pre-set goals of the programme. (IUCN/SSC, 2013)

4.6 MacDonald's Seven Questions for Reintroductions

4.6.1 Introduction

From 18 different studies, collected and presented in the book by Hayward and Somers (2009a), about the reintroduction of top-order predators, MacDonald (2009) posed the question "what general view of carnivore reintroductions emerges?". From his attempts to answer this question, seven further questions emerged which were published with the aim that they act as a framework for future carnivore reintroduction work. Using examples from across the taxa, these seven questions are of aim to be used by other conservationists to alleviate pitfalls that can cause the failure of a reintroduction programme and hence, waste many resources (MacDonald, 2009). These questions will be used as an assessment of this study and its suggestions. Each answer will be given using the findings of this study and prior scientific knowledge of the Amur leopard and Siberian tiger, but importantly with a focus on an ecological perspective, rather than the political aspects. Where an answer cannot be given, or future work is required, this will be identified. Many suggestions and results of this study may act as answers to multiple questions and therefore may appear repetitive. The repetition has been included as it allows each question and answer to stand alone, separate of each other.

4.6.2 The Questions

Is Reintroduction the Right Solution?

Reintroductions are considered to be a last resort (Abell *et al.,* 2013). The establishment of a second population of Amur leopard is regarded as a necessity, with the extremely limited gene pool the reason (WCS, 2001). This second population would be isolated from the existing wild population and could be created using via reintroduction of captive bred individuals, from whom a new gene pool can be established. Translocation of wild individuals would not be a feasible alternative as it is the establishment of this new gene pool that is essential for the Amur leopard.

Although Siberian tiger populations have increased since the 1990s and are now stable, their status remains at endangered (Goodrich *et al.,* 2016). As much as 93% of their range is co-inhabited with humans and the need for new protected regions or TCLs is fundamental to their long-term survival (Goodrich *et al.,* 2010). While many TCLs have been suggested in the Siberian tiger range, more are needed. The establishment of a new population, in the suggested region that can be protected and classified as a TCL, will help to increase these dangerously low numbers. Unlike for the Amur leopard, the translocation of wild Siberian tiger individuals may be the more feasible option, with individuals collected from various parts of their range to create this new population.

With both species as acting as apex predators in their habitats, the loss of each would be felt throughout the trophic levels, having a huge effect on biodiversity. The establishment of the new populations suggested in this study would aid in solidifying each predators' respective numbers.

Has the Bigger Picture Been Properly Evaluated?

Although reintroductions of the Siberian tiger and the Amur leopard are considered to be part of the solution to their survival, they may not be feasible long-term. Since their localised extirpation, science and society has changed. Rather than attempting to re-establish past communities, which may not be prudent, instead, we should be aiming to creating a new future for the ecosystem (MacDonald, 2009). Conservation programmes include both science and policy and hence encompasses politics. Although politics will not be considered or discussed in depth here, a basic understanding is needed. "Futuristic restoration" is a term used for these conservation programmes which encompasses the dynamics of change (Choi, 2004). It is suggested by Harris *et al.* that the future of the ecosystem (ecological integrity) should be the focus of any long-term plan for conservation, to incorporate climate change, land-use change, political changes and other changes (Harris *et al.,* 2006).

The establishment of strictly protected conservation parks/reserves will aid in the prevention of anthropogenic land change but the impacts that climatic change, along with other ecological impacts, will have should be among the next things to be investigated. Analysis of the vulnerability of forested regions to climate change is essential to the conservation future of the Siberian tiger and the Amur leopard. While the identified regions may be considered highly suitable now, this may not be the case if current climatic predictions continue, and we need to consider this possibility.

On What Scale is it Worthwhile to Conduct a Reintroduction if it is to be a Priority for Biodiversity Conservation?

It may seem intuitively that the larger the scale, the more beneficial the conservation programme. Although a large scale may be considered the best, this is not always so (MacDonald, 2009). Scales can vary, with reintroductions occurring in both large protected areas and smaller private areas. Many of these programmes are designed as expansive, aimed at requiring minimal intervention as the species naturally expands beyond the initial reintroduction site. These are considered to among the best such scheme but require extremely large protected areas (Frankham, 2009).

Suitable habitat availability, ecological corridors, carrying capacity estimations and gap analysis all help to determine the scale that would be required for the Siberian tiger and the Amur leopard. The large geographical area of each region allows for population expansion, while the carrying capacity demonstrates the number each region might support. With Amur leopard reintroduction requiring captive bred individuals, genetic analysis would be needed to ensure that this second population remains genetically different to the current wild one. The final assessment will however depend upon the classification of the regions as protected with the necessary followings.

Has Society the Capacity to Cope with the Challenged of Reintroduction and to Take up the Benefits?

Human society is an essential part of modern-day conservation programmes, however, as in assessing the bigger picture, human affairs can be complex and difficult to predict. To help alleviate this, adaptable contingency plans are a necessity (MacDonald, 2009). Only with cooperation from these local people can reintroductions be successful (Setchell *et al.,* 2016). Otherwise, schemes can fall victim to various unforeseen problems, including the failure to anticipate poor public acceptance of the reintroduced species; a failure to prevent human-predator conflicts; a failure to educate and dispute the historic thought that predators are ‘bad’; and a failure to install an alternative economical opportunity to replace those lost in designated reintroduction areas (MacDonald, 2009).

The extreme successes seen in carnivore biosocial conservation programmes in the past demonstrate their effectiveness (Hazzah *et al.,* 2009; Mishra *et al.,* 2003). As part of future work, conservations should take place with local people, to understand their thoughts. Questions about their fears of the Siberian tiger and Amur leopard and the potential effect that these animals could have upon their livelihood will probably be important and should be carefully considered. An understanding of locals’ wants for the project will determine the overall success of the reintroduction. Without these local people on board, there is an extremely high chance that the reintroduction of both species will fail.

What is the Missing Science and why?

Conservation biology should be founded on evidence, but this is not always the case, often it is disregarded. There may also be knowledge gaps, but these should be identified prior to the programme, rather than after (MacDonald, 2009). However, these gaps may not be noticed till it’s too late.

The suggestions made in this study, along with this discussion of the possible subsequent conservation actions, are not a definite statement or final plan for the reintroduction of the Siberian tiger and Amur leopard. Instead, this work aims to act as a stepping stone or launch pad for further work, using its findings as a direction. Each step can evaluate and identify the gaps in a specific area. Localised movement of prey, for instance, was not included in this study, as we aimed instead to identify the potential variety of prey present. This is an example of some missing science and could be a focus for one of the next steps. The opinions of local people can also be included as part of the missing science and again, should be a future focus.

What is the Role of Animal Welfare?

Ranging from the welfare of reintroduced individuals to their impacts on other species within the reintroduction regions, the role of animal welfare is one that should be included in conservation programmes (MacDonald, 2009). Although wild Siberian tigers may be used for reintroduction, which is widely considered to be the ideal option, captive-bred Amur leopards will be required. This raises many considerations for their welfare. They may lack the necessary skills required of their wild-born counterparts which could result in injuries from exposure to novel environments and damage caused by humans or other species which they have no learnt knowledge of.

The inclusion of competition between reintroduced tigers and leopards demonstrates an initial consideration for welfare in this study. The smaller Amur leopard is often displaced and outcompeted by the much larger Siberian tiger (Wang *et al.,* 2017). Selecting two reintroduction regions separate from each other means that each population can grow without the initial worry of competition. This competition is a natural part of the both species biology, but its avoidance at this early stage will aid in establishing sustainable populations. Breeding programmes would have to be heavily monitored in attempting to teach the skills that these animals will need in the wild including the ability to hunt, shyness to humans and avoiding other, larger predators (Christie, 2009). This will inevitably have multiple steps, each providing new information.

Whether the Generalizations Adequately Prescribe the Particular?

The IUCN among others provide many criteria and suggestions that should be considered during reintroduction programmes. Although these allow for the construction of a solid plan, it can be at the detriment to the actual need of the species or the actual aim of the study (MacDonald, 2009). Every species is different and occupies a different niche. This can also be true of different populations of the same species. While using suggestions and findings from this study and the necessary future work, the aim should remain re-establishing the Siberian tiger and Amur leopard, rather than trying to meet any other criteria. There is not always a single answer to the questions presented in conservation programmes, multiple answers will arise. Previous work and frameworks will undoubtedly provide much valid support, but fine-tuning of these is essential, using biology and evidence about the target species and including local views and socio-economic circumstances (MacDonald, 2009).

Throughout this study the focus has remained on the Siberian tiger and the Amur leopard respectively. Various criteria, suggestions and frameworks have been used as evaluations of the findings rather than attempting to find results that fit. There is still much information that must be gathered as part of this on-going programme, but the fore-ground consideration must remain with the species and local people. This is the only way reintroductions of Siberian tiger and Amur leopards will be successful.

4.7 Action Plans

Throughout this study, much new information has been gathered regarding the identification of suitable habitats and regions with potential to support Siberian tiger and Amur leopard reintroductions. To help conclude this work and set out future steps, a series of action plans will be presented. These will first present the findings and then put them into the greater context and making future conservation suggestions.

4.7.1 Siberian Tiger Findings

- Using various biotic and abiotic variables, suitability modelling revealed almost 30,000 km^2 of new suitable Siberian tiger habitat, all within its historical distribution. This could potentially increase the current distribution of 95,730 km^2 (as put forth by Goodrich *et al.* (2015)), by 31%, to 125,396 km^2.
- The suitability model revealed 24 areas which can be grouped into 4 separate regions. Of these, the region located in Primorski Krai and Heilongjiang that offers the highest suitability value and therefore, the most potential for a reintroduction. The region makes up 14,000 km^2 of the suitable Siberian tiger habitat and has a potential carrying capacity for 50 breeding individuals.
- As well as the region recommended for a reintroduction, a further region was identified as having potential as a future area for reintroduction. 6,628 km^2 of suitable habitat was identified in Khabarovsk Krai and the Jewish Autonomous

Oblast (JAO). This region does not offer the same suitability of the suggested reintroduction region, it does however have the lowest human impact value. As this region exists in the historical distribution of the Siberian tiger, I suggest this region for future research to discover its potential. The low human impact values represent huge potential as a future stronghold.

4.7.2 Amur Leopard Findings

- The suitability model, using multiple biotic and abiotic variables, revealed more than 22,000 km^2 of suitable Amur leopard habitat. This has potential to increase the current distribution, 12,206 km^2 (Miquelle *et al.,* 2011) by 181%, taking the leopard's range to over 34,300 km^2.
- 18 individual areas were taken from the suitability model and could be separated into 4 regions, all within the Russian Far East, north eastern China and the DPR Korea. It was the region in Jilin and the DPR Korea that provided the highest suitability, providing 9,149 km^2 of potential habitat. This region would have the capacity to potentially support 89 breeding individuals. This alone could almost double the wild Amur leopard population.

4.7.3 Action Plans and the Next Steps

Whilst the findings of this study offer a bright future for the conservation of the Siberian tiger and the Amur leopard, these numbers and figures would not be achievable without a vast amount of further work and considerations. Whilst this thesis has not attempted to give answers for this further work, it has attempted to make suggestions about possible outcomes or where the next line of research should be. These action plans will give an overview of this.

- Within each suggested region, many of the individual areas are fragmented from each other by the presence of major roads, which act as a barrier for dispersal. The installation of ecological corridors would help in removing these barriers. Least-cost path analysis found potential corridors between each of the suggested areas however many will involve crossing of these major roads. Ecological bridges have been used for other species in other global locations that have aided this problem. Further localised analysis of the road network in and around these suggested areas may help to identify the parts of the roads that will serve as the best location for an ecological bridge or some other method of road crossing.

- Poaching is one of the largest causes of fatalities for both the Siberian tiger and the Amur leopard, therefore strictly protected nature reserves or national parks, with active rangers will help to protect the individuals released into these new regions. This would prevent minimal interactions with people and reduce poaching.
- All of the suggestions made during this study would be useless if the local people are not consulted and included in the planning stages. Unfortunately, much of both the Siberian tiger and Amur leopard's fatalities are linked to people. This can be through deforestation of their habitat, direct poaching of the big cat species and killings in retaliation of the loss of livestock. For both species to succeed in these new, suggested, reintroduction areas, these fatalities must ideally stop, or at least reduce drastically. Continuing with already set up programmes as well as using other plans as examples, discussions with local people about compensation programmes can help with the retaliation killings, understanding what the local people want and need must be included in these plans. The Lion Guardians organization in Africa is also an example which can be implemented in these new areas. Paying local people to protect these species, will give them incentive and replace the money they previously got through poaching and deforestation.
- The trans-border nature of the two conservation priorities suggested in this study would also require a level of international cooperation. Country borders are an anthropogenic distinct entity and do not exist for these species, therefore they would not prevent cross border movement and protection on a single side of the border would be largely useless.

- There is still much knowledge that is still unknown regarding both the Siberian tiger and the Amur leopard. Work should be continuing, using different techniques and including variables. This should include both modelling work done for afar, and also localised work, surveying the suggested areas determining how suitable and practical they are.
- The work conducted in this study can be also be used as a basis for other endangered large carnivore species. Using the key drivers and attempting to model these will allow for the discovery of new areas that could be used as potential reintroduction sites. Significantly endangered carnivores, like the Florida panther (*Puma concolor cougoar*) and the Ethiopian wolf (*Canis simensis*) could both significantly benefit from a similar study, where new areas within their historical distribution could be suggested for reintroduction.

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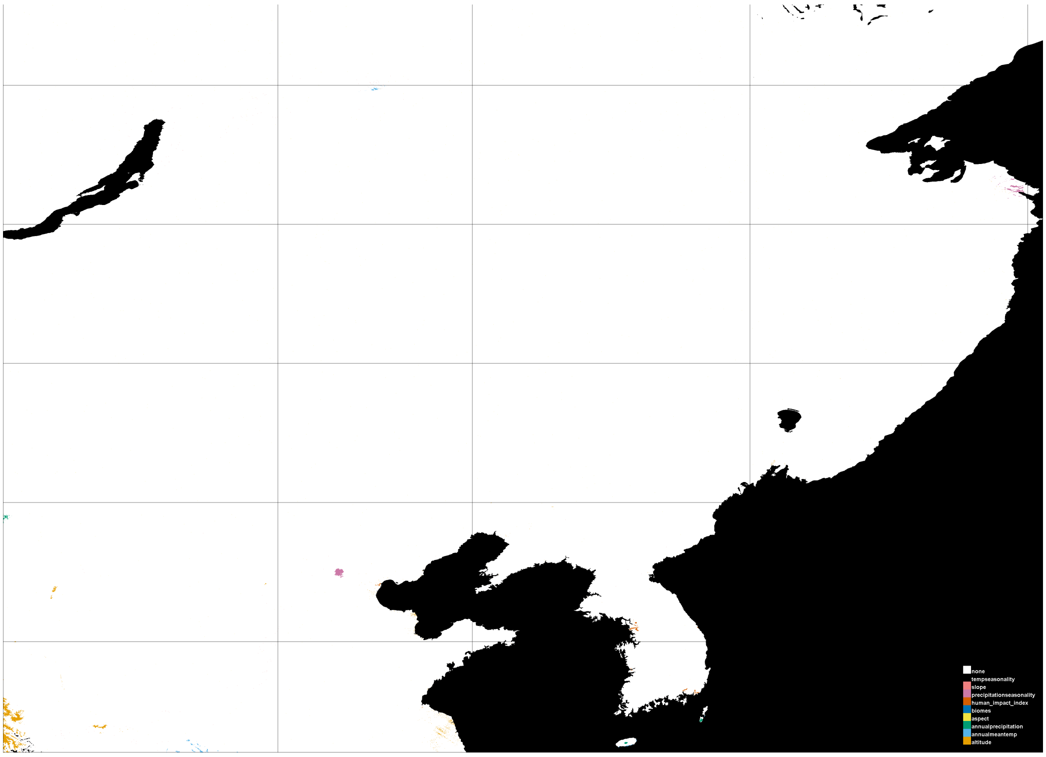
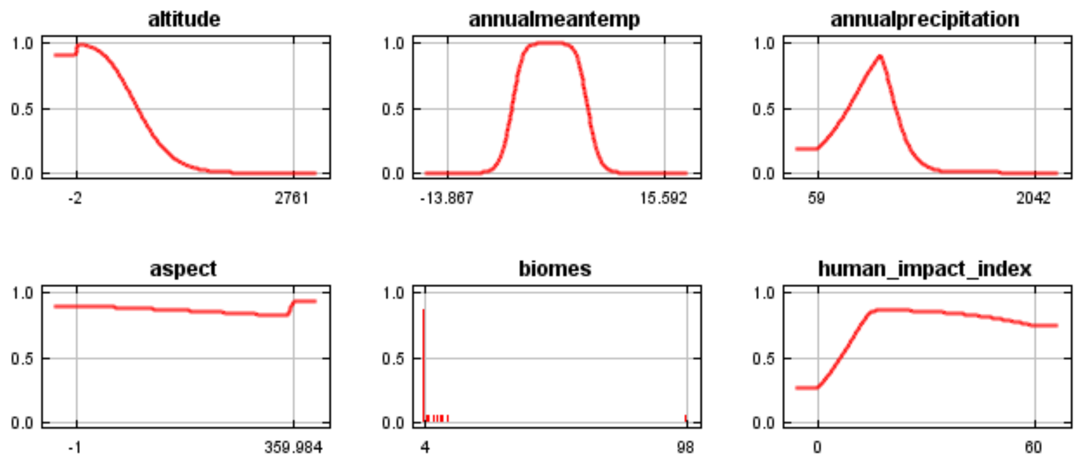
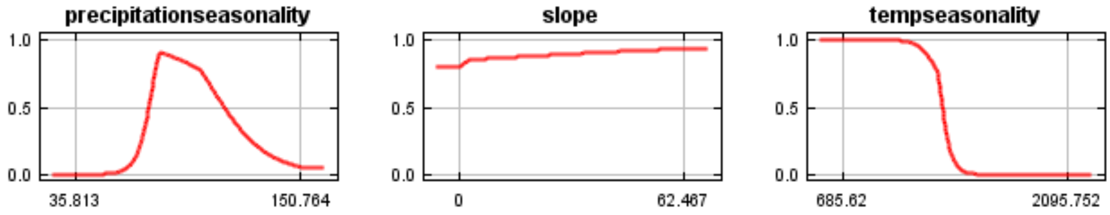
Appendix 1.



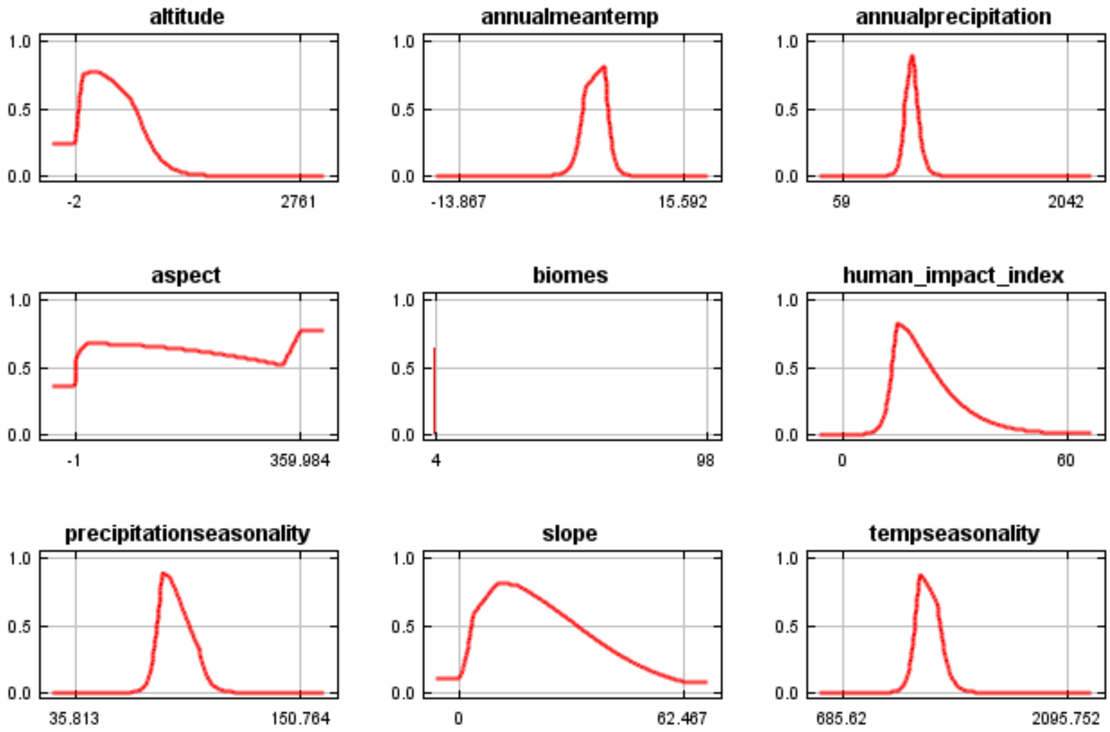
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together.





In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.



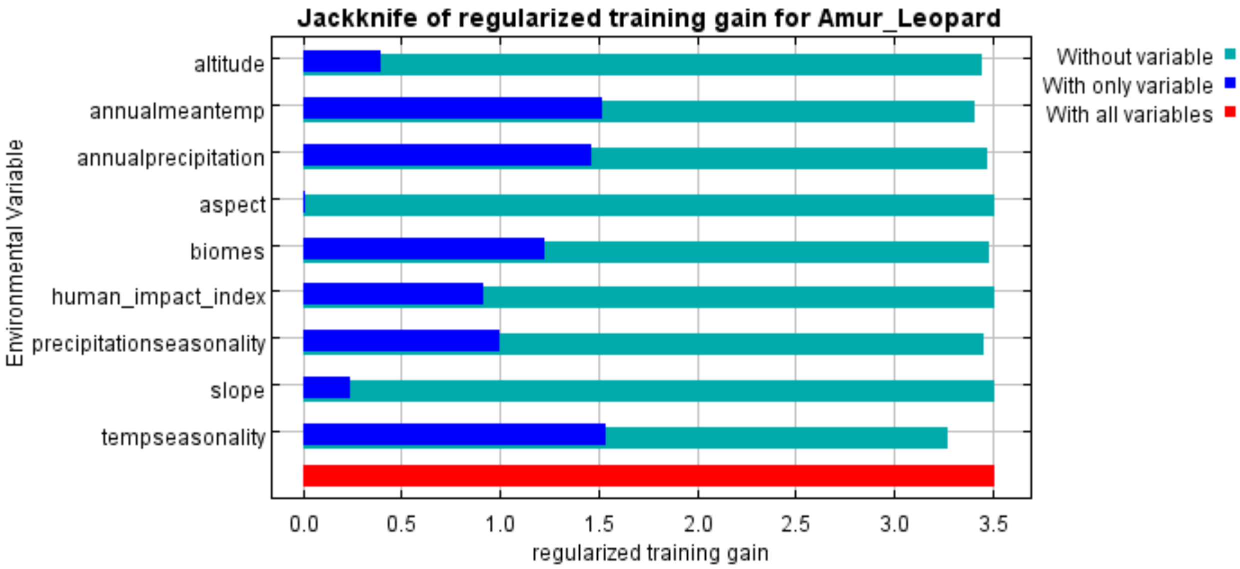
Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated.

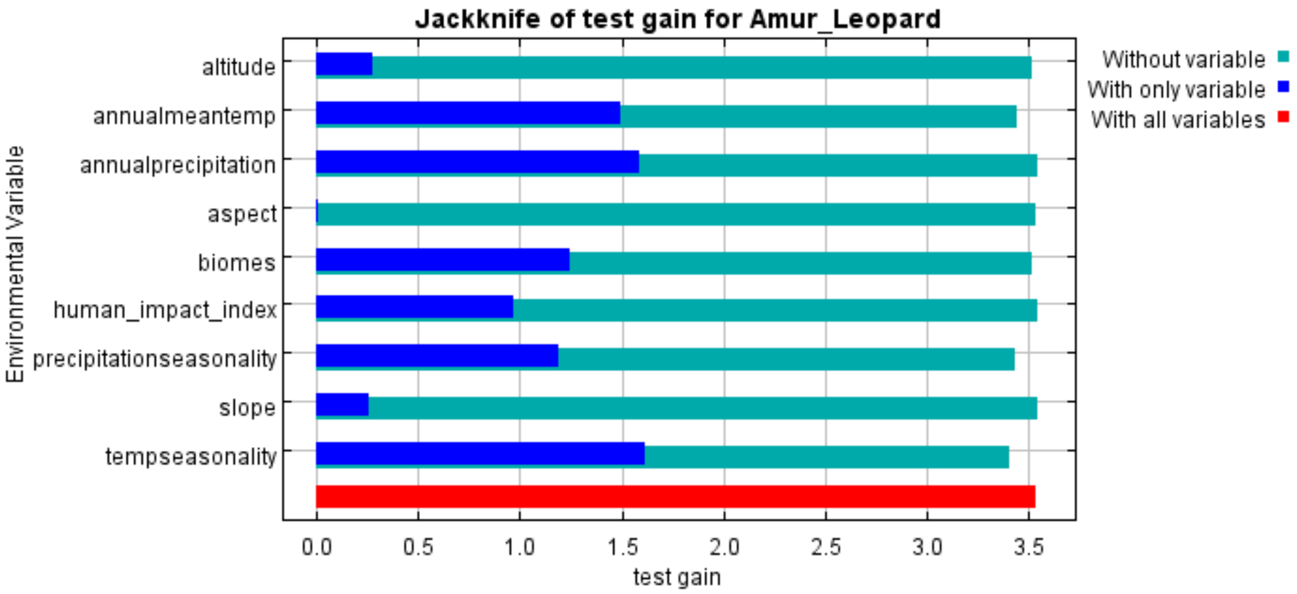
Variable	Percent contribution	Permutation importance
biomes	34.2	2.8

annualmeantemp	19.9	36.5
tempseasonality	17.4	52.6
precipitationseasonality	14.5	1.6
human_impact_index	7.1	0.5
altitude	5	5
annualprecipitation	1.8	0.8
slope	0.1	0
aspect	0.1	0.1

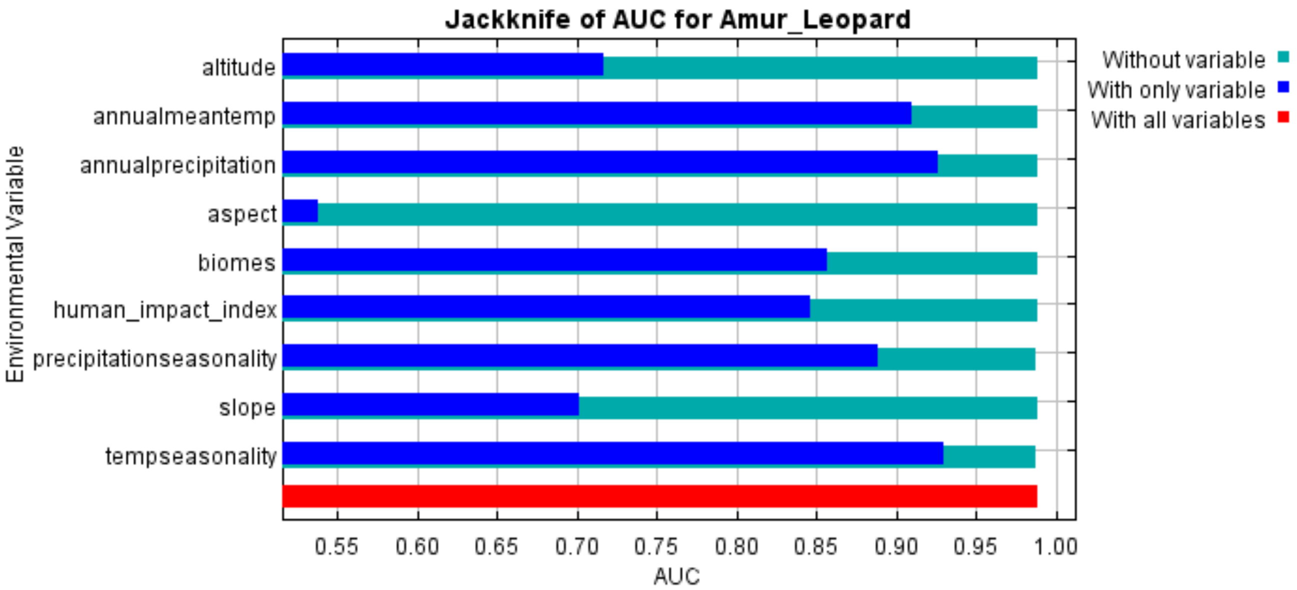
The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is tempseasonality, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is tempseasonality, which therefore appears to have the most information that isn't present in the other variables.



The next picture shows the same jackknife test, using test gain instead of training gain. Note that conclusions about which variables are most important can change, now that we're looking at test data.



Lastly, we have the same jackknife test, using AUC on test data.



Raw data outputs and control parameters

The data used in the above analysis is contained in the next links. Please see the Help button for more information on these.
The model applied to the training environmental layers
The model applied to the environmental layers in E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
The coefficients of the model
The omission and predicted area for varying cumulative and raw thresholds
The prediction strength at the training and (optionally) test presence sites
Results for all species modeled in the same Maxent run, with summary statistics and (optionally) jackknife results

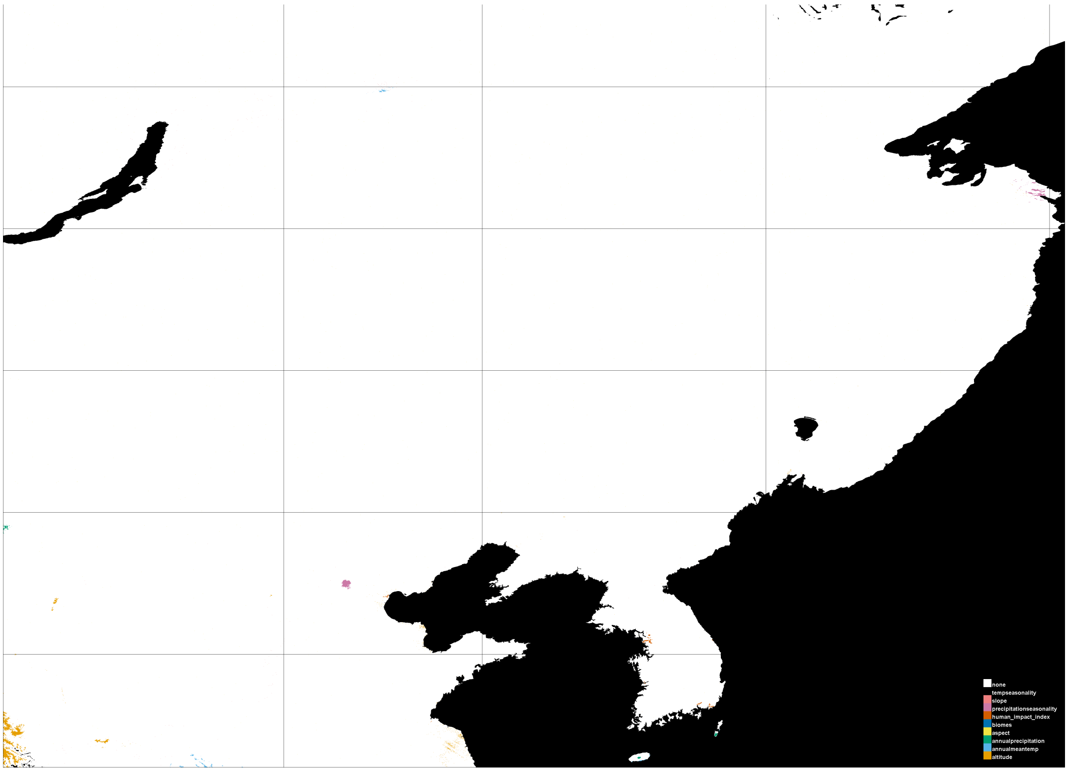
Regularized training gain is 3.515, training AUC is 0.991, unregularized training gain is 3.720.
Unregularized test gain is 3.534.

Test AUC is 0.989, standard deviation is 0.002 (calculated as in DeLong, DeLong & Clarke-Pearson 1988, equation 2).
Algorithm converged after 740 iterations (13 seconds).

The follow settings were used during the run:
147 presence records used for training, 48 for testing.
10147 points used to determine the Maxent distribution (background points and presence points).
Environmental layers used: altitude annualmeantemp annualprecipitation aspect biomes(categorical) human_impact_index precipitationseasonality slope tempseasonality
Regularization values: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500
Feature types used: hinge product linear quadratic
responsecurves: true
jackknife: true
outputdirectory: E:\Modelling\Maxent_Files\Amur_Leopard_Outputs\Run25(All_Points_Jackknife
projectionlayers: E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
samplesfile: E:\Modelling\Output models\scratch\Jiang_LLNP_Merge_TableToExcel.csv
environmentallayers: E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
randomtestpoints: 25
maximumiterations: 5000
Command line used:

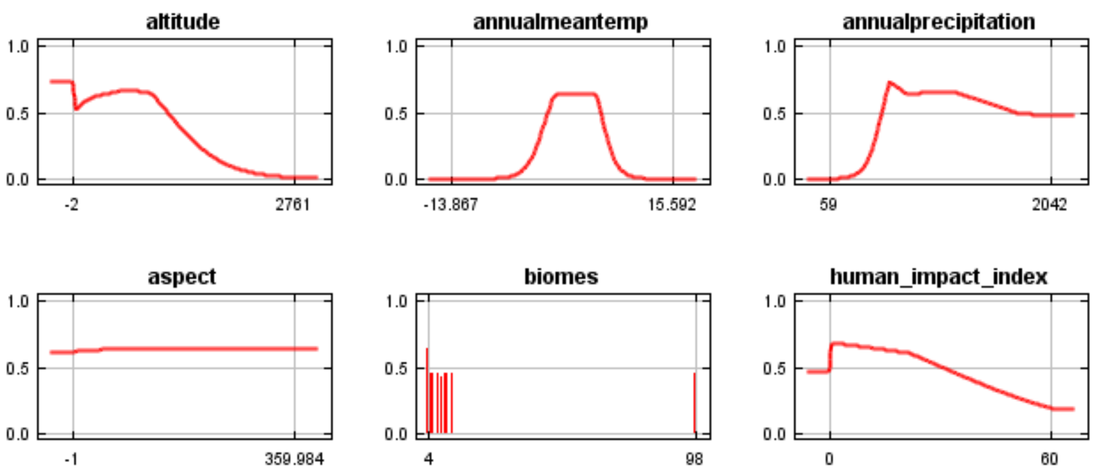
Command line to repeat this species model: java density.MaxEnt nowarnings noprefixes -E "" -E Amur_Leopard responsecurves jackknife outputdirectory=E:\Modelling\Maxent_Files\Amur_Leopard_Outputs\Run25(All_Points_Jackknife projectionlayers=E:\Modelling\Maxent_Files\ASCII_Environmetal_layers "samplesfile=E:\Modelling\Output models\scratch\Jiang_LLNP_Merge_TableToExcel.csv" environmentallayers=E:\Modelling\Maxent_Files\ASCII_Environmetal_layers randomtestpoints=25 maximumiterations=5000 -N ecoregions -N prey -t biomes

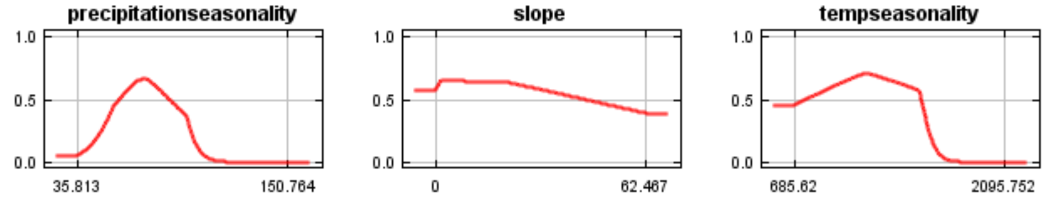
Appendix 2.



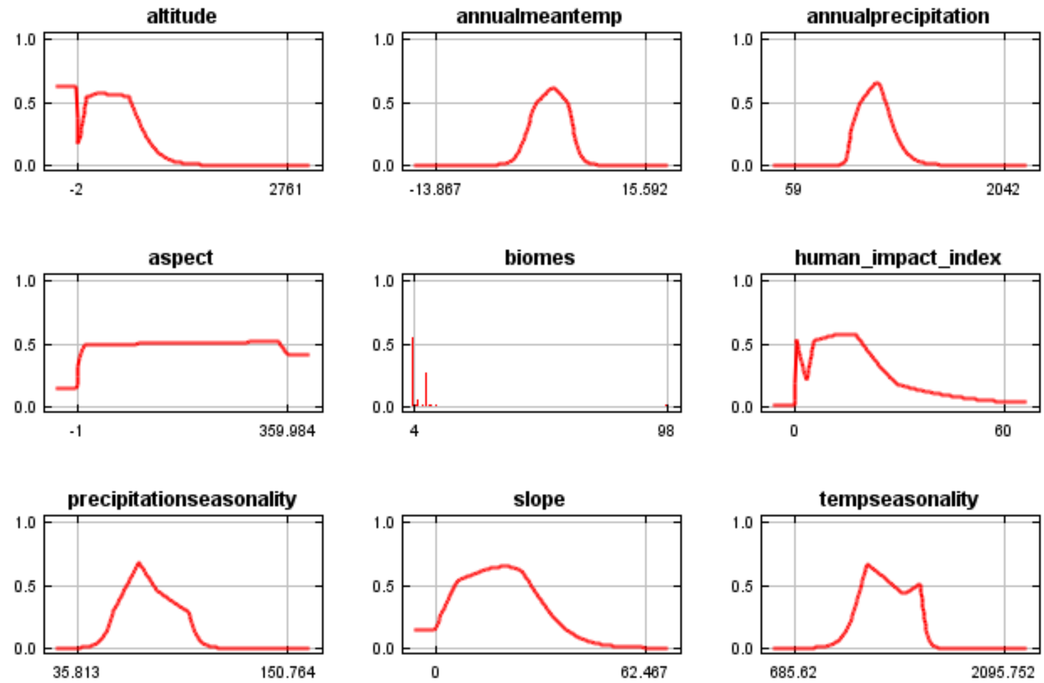
Response curves

These curves show how each environmental variable affects the Maxent prediction. The curves show how the predicted probability of presence changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. Click on a response curve to see a larger version. Note that the curves can be hard to interpret if you have strongly correlated variables, as the model may depend on the correlations in ways that are not evident in the curves. In other words, the curves show the marginal effect of changing exactly one variable, whereas the model may take advantage of sets of variables changing together.





In contrast to the above marginal response curves, each of the following curves represents a different model, namely, a Maxent model created using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by correlations between the selected variable and other variables. They may be easier to interpret if there are strong correlations between variables.



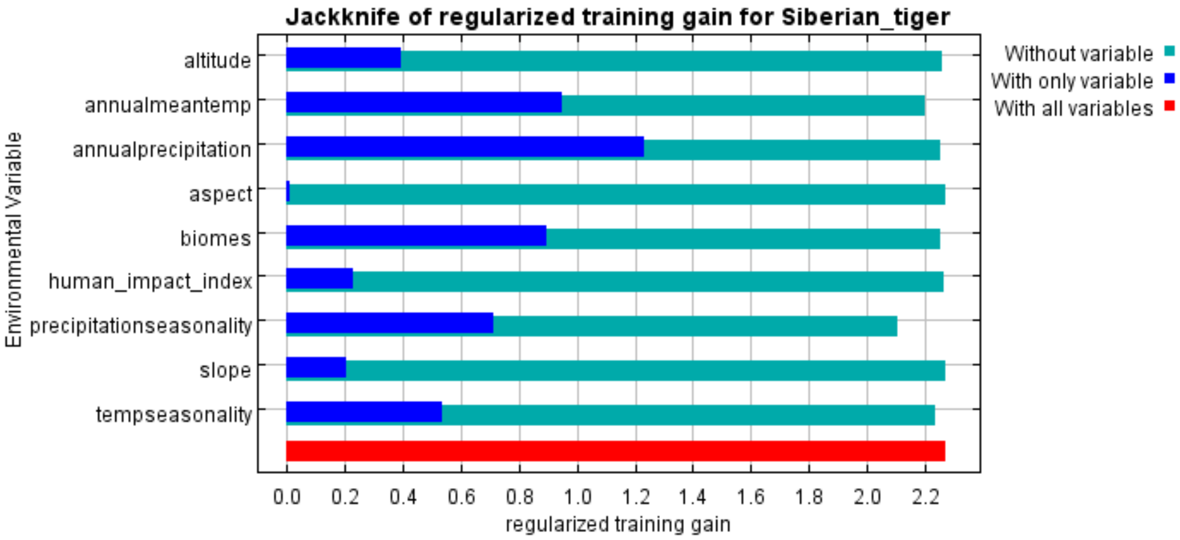
Analysis of variable contributions

The following table gives estimates of relative contributions of the environmental variables to the Maxent model. To determine the first estimate, in each iteration of the training algorithm, the increase in regularized gain is added to the contribution of the corresponding variable, or subtracted from it if the change to the absolute value of lambda is negative. For the second estimate, for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. As with the variable jackknife, variable contributions should be interpreted with caution when the predictor variables are correlated.

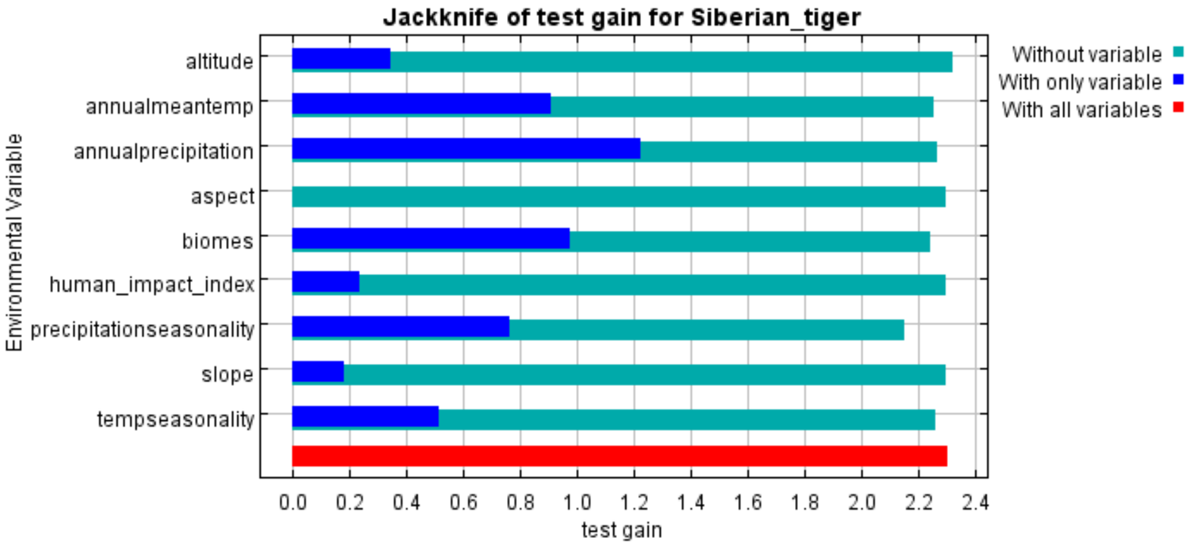
Variable	Percent contribution	Permutation importance
biomes	38.8	1.1

annualmeantemp	23.8	37.1
precipitationseasonality	19	30.5
annualprecipitation	9.1	10.1
tempseasonality	6.3	18.2
altitude	2.5	2.1
human_impact_index	0.3	0.7
slope	0.1	0
aspect	0	0.1

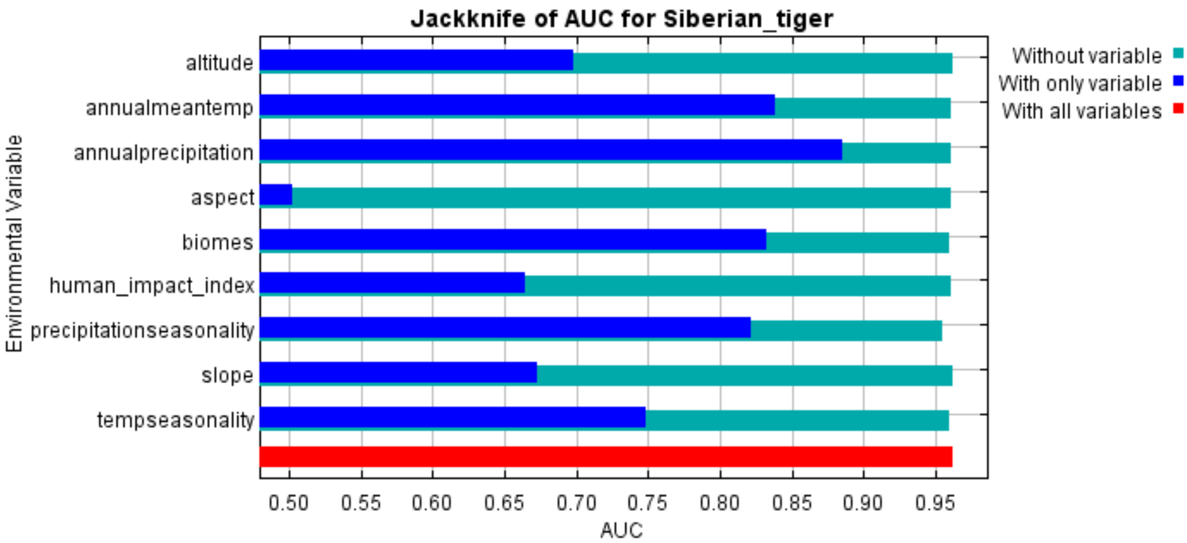
The following picture shows the results of the jackknife test of variable importance. The environmental variable with highest gain when used in isolation is annualprecipitation, which therefore appears to have the most useful information by itself. The environmental variable that decreases the gain the most when it is omitted is precipitationseasonality, which therefore appears to have the most information that isn't present in the other variables.



The next picture shows the same jackknife test, using test gain instead of training gain. Note that conclusions about which variables are most important can change, now that we're looking at test data.



Lastly, we have the same jackknife test, using AUC on test data.



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The model applied to the environmental layers in E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
The coefficients of the model
The omission and predicted area for varying cumulative and raw thresholds
The prediction strength at the training and (optionally) test presence sites
Results for all species modeled in the same Maxent run, with summary statistics and (optionally) jackknife results

Regularized training gain is 2.274, training AUC is 0.965, unregularized training gain is 2.380.
Unregularized test gain is 2.299.

Test AUC is 0.962, standard deviation is 0.003 (calculated as in DeLong, DeLong & Clarke-Pearson 1988, equation 2).
Algorithm converged after 820 iterations (15 seconds).

The follow settings were used during the run:
458 presence records used for training, 152 for testing.
10457 points used to determine the Maxent distribution (background points and presence points).
Environmental layers used: altitude annualmeantemp annualprecipitation aspect biomes(categorical) human_impact_index precipitationseasonality slope tempseasonality
Regularization values: linear/quadratic/product: 0.050, categorical: 0.250, threshold: 1.000, hinge: 0.500
Feature types used: hinge product linear quadratic
responsecurves: true
jackknife: true
outputformat: logistic
outputdirectory: E:\Modelling\Maxent_Files\Siberian_Tiger_Outputs\Run16(Combi_Log_Jackknife)
projectionlayers: E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
samplesfile: E:\Modelling\Maxent_Files\Combi_Tiger.csv
environmentallayers: E:\Modelling\Maxent_Files\ASCII_Environmetal_layers
randomtestpoints: 25
maximumiterations: 5000
Command line used:

Command line to repeat this species model: java density.MaxEnt nowarnings noprefixes -E "" -E Siberian_tiger responsecurves jackknife outputformat=logistic outputdirectory=E:\Modelling\Maxent_Files\Siberian_Tiger_Outputs\Run16(Combi_Log_Jackknife) projectionlayers=E:\Modelling\Maxent_Files\ASCII_Environmetal_layers samplesfile=E:\Modelling\Maxent_Files\Combi_Tiger.csv environmentallayers=E:\Modelling\Maxent_Files\ASCII_Environmetal_layers randomtestpoints=25 maximumiterations=5000 -N ecoregions -N prey -t biomes