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Implications of the shared socioeconomic pathways for tiger (*Panthera tigris*) conservation

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ABSTRACT

Over the last century, numbers of wild tigers (*Panthera tigris*) have crashed, while human populations have boomed. Here we investigate future trajectories of human population within tiger range through analysis of the shared socio-economic pathways (SSPs). These five pathways describe urban, rural and total population distributions by decade through 2100, based on plausible but contrasting scenarios of economic, education, migration, and urbanization policy. In 2010 approximately 57 million people lived in regions defined as "tiger conservation landscapes" (or TCLs); 8% of sympatric people lived in towns and cities that occupied 4% of tiger range. We show that tigers could share these same geographies with as few as 40 million (30% decline compared to 2010) or as many as 106 million people (an increase of 85%) by 2100. Those populations could be as much as 64%, or as little as 17%, urbanized, depending on the pathway. Urban areas are likely to expand, displacing between 6 and 22% of tiger's current range, depending on how urban growth is managed. Human population density thresholds compatible with tigers vary by region, from 140 persons/km^2 in the Indian subcontinent, to 10 persons/km^2 in the Russian Far East and northern China. SSP3, a future where nations indulge regional rivalries, would make conservation more difficult, whereas SSP1, with a focus on well-managed urbanization and education, could help relieve pressures. Tigers are a conservation-reliant species and will likely remain so through the 21st century, therefore we suggest coupling continued site-level protection with efforts to develop constituencies for conservation in Asia's burgeoning cities.

1. Introduction

Tigers (*Panthera tigris*) are an endangered apex predator currently threatened by human activities across Asia, from the Indian subcontinent to the Russian Far East (Goodrich et al., 2015). For most of the twentieth century, it appeared that wild tigers were on an inexorable path toward extinction (Fig. 1), similar to other large carnivores (Wolf and Ripple, 2017). Tigers were extirpated from Bali in the 1950s, from Java in the 1970s, and riparian habitats in Central Asia in the 1980s (Seidensticker et al., 1999). During the twentieth century large portions of range were lost in formerly prime habitat in China (Kang et al., 2010), India (Schaller, 1974), and Southeast Asia (Lynam and Nowell, 2011). By the mid-1990s, Seidensticker et al. (1999) estimated that only 5000–7000 tigers remained in the wild, down from perhaps 100,000 at the beginning of the twentieth century (Nowell and Jackson, 1996). An assessment in 2007 found that tigers had lost some 93% of their range (Dinerstein et al., 2007) and the remaining 7% consisted of 76 isolated tiger conservation landscapes (TCLs). A reanalysis by Walston et al. (2010) suggested that the situation was even more dire; remaining breeding tiger populations were restricted to as few as 42 "source sites" (SSs), which represented as little as 0.5% of the historical range (circa 1900). A combination of survey data and expert opinion about tiger density and occupied area suggested that < 3200 tigers lived in the wild ten years into the new millennium.

While tiger populations have crashed, the human population of Asia has boomed (Fig. 1). When tigers were described by Linneaus in 1758, Asia was home to approximately 500 million people (Livi-Bacci, 2012). The human population grew to around 790 million by 1850, and then nearly doubled to 1.37 billion by 1950. Today, the population of Asia stands at over 4.44 billion (United Nations - Department of Economic and Social Affairs - Population Division, 2017), a tripling since the 1950s and nearly a nine-fold increase since the 18th century. In recent

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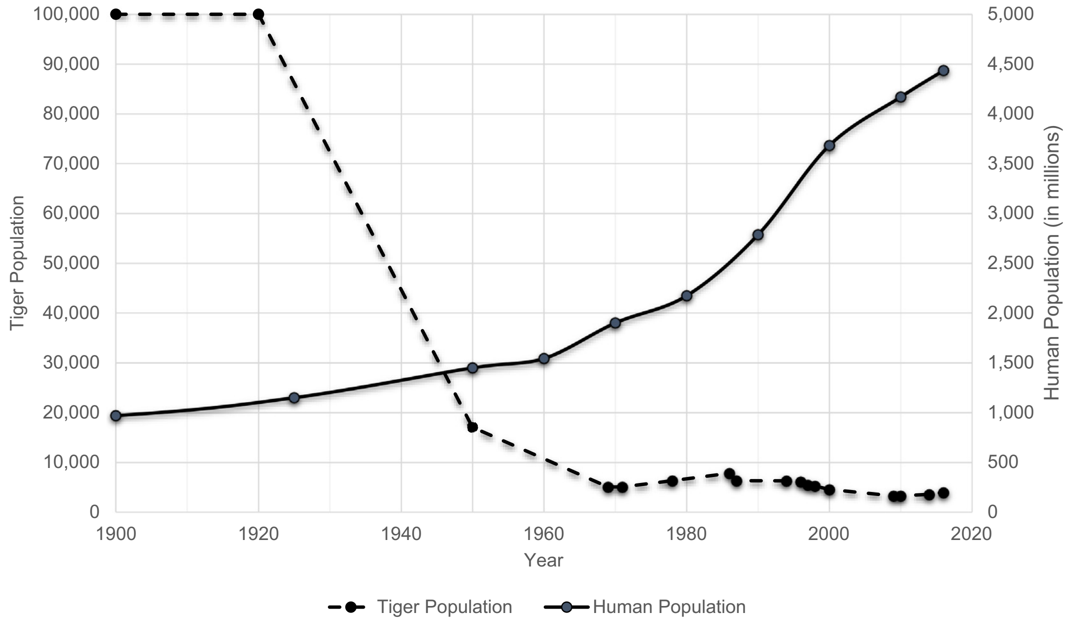

Fig. 1. Populations of people and wild tigers in Asia 1900–2015.

decades, Asian economic growth has propelled hundreds of millions of people out of poverty and into the middle class (Chen et al., 2015). Much of that economic growth is the result of urbanization, in which formerly rural populations find better paying work in non-agricultural, urban sectors connected to the global economy, particularly manufacturing (Seetharam, 2010; Yang, 2013). The movement from countryside to city in China has been described as the largest migration in human history (Miller, 2012), where the urban fraction of the population has increased from 23% to 55% of the population over the last thirty years (United Nations - Department of Economic and Social Affairs - Population Division, 2015). As a consequence of urbanization, improved economic conditions, and better education, mortality and fertility rates have fallen, driving the demographic transition (Montgomery and Balk, 2017). These conditions are creating the prospects for population stabilization in the twenty-first century for many countries in the tiger's range (Choe, 2017; Lutz and KC, 2017), with profound consequences for biodiversity conservation in Asia (Sodhi et al., 2004; Hughes, 2017) and the world (Allendorf and Allendorf, 2012; Crist et al., 2017; Sanderson et al., 2018).

Here we examine one aspect of the future of tigers through analysis of possible human population trajectories over the course of the 21st century. Recently a group of climate scientists, social scientists and geographers, working on behalf of the Intergovernmental Panel on Climate Change, developed five shared socioeconomic pathways (SSPs) (O'Neill et al., 2017). These pathways describe five plausible scenarios, labelled SSP 1–5, of future social conditions in terms of demography, economy, technology, governance, and international trade and migration. The SSPs are qualitative narratives of possible futures on which quantitative expressions of population can be developed by modifying demographic and spatial-extrapolation models to project future population distributions. For example, Jiang and O'Neill (2015) reported projections of future urbanization patterns at the national scale based on the SSPs, and KC and Lutz (2017) produced national demographic estimates of urban and rural population. Jones and O'Neill (2016) used the demographic projections from KC and Lutz (2017) to construct spatially explicit global population maps of urban and rural populations for each decade from 2010 to 2100. These maps, described in detail below, are of sufficient spatial resolution that they provide a basis for projecting how human populations may change over the course of the 21st century in areas critical for tiger conservation.

Human-tiger interactions depend not only on the relative size of the populations, but the choices people make about consumption and conservation. Currently a major threat to this species is poaching for the illegal trade in tiger parts, including skin, bones, meat and tonics, which are reputed to have medicinal qualities (Nowell and Xu, 2007; Guynup, 2014). The main driver of the trade is the market for traditional medicines, particularly in Chinese cities, which have become much more affluent than in the past (Gratwicke et al., 2008; Walston et al., 2016). Simultaneously, in the rural locales where tigers live, conversion for agriculture and forest production, commercial logging, and expansion of human settlements continue to drive loss and fragmentation of tiger habitat (Bateman et al., 2010; Goodrich et al., 2015). Many of these raw materials are transformed into goods to build and sell in cities (Asian Development Bank, 2014). Sympatric tigers and people in rural areas also come into direct conflict; tiger sometimes prey on livestock and attack people, often leading to retaliatory killings (Karanth and Gopal, 2005). Meanwhile hunting of tiger prey animals in rural areas (typically, large ungulate species) lowers the value of otherwise intact habitats through indirect competition (Karanth et al., 2004).

Conservationists thwart threats to tigers largely through protection of SSs within larger conservation landscapes (Stokes, 2010; Walston et al., 2016). If poaching can be curbed, habitat secured, and prey populations allowed to rebound, then tiger populations have the potential to recover quickly (Miquelle et al., 2015). Landscape-scale efforts to slow habitat loss, minimize conflict, maintain corridors, and alter extractive industry are also underway (Yumnam et al., 2014). Concurrent efforts in urban markets focus on decreasing demand for tiger parts through education and law enforcement. Recent reports of global tiger population increases (WWF and GTF, 2016), while considered over-optimistic by some (e.g. Karanth, 2016), reflect a sense that the conservation situation for tigers is changing and, at least in some places, possibly for the better, for the first time in over a century.

The objectives of our paper are as follows: (1) to determine how human populations may change in tiger range with respect to the different SSPs during the 21st century; (2) to investigate thresholds of human population density in areas critical for human-tiger interactions; and (3) to suggest how socioeconomic policies with respect to demographic transition may influence the future of tiger conservation.

Table 1
Estimates of human population sharing tiger range during 21st century based on spatial projections (Jones and O'Neill, 2016) of the shared socioeconomic pathways (SSPs; O'Neill et al., 2017), with the predicted peak population highlighted in **bold** type.

Year	SSP 1			SSP 2			SSP 3			SSP 4			SSP 5		
	Pop.[a]	Pop. urban[b]	Area urban[c]	Pop.[a]	Pop. urban[b]	Area urban[c]	Pop.[a]	Pop. urban[b]	Area urban[c]	Pop.[a]	Pop. urban[b]	Area urban[c]	Pop.[a]	Pop. urban[b]	Area urban[c]
2010	57.2	8	4	57.2	8	4	57.2	8	4	57.2	8	4	57.2	8	4
2020	61.2	12	5	63.2	10	4	64.8	9	4	62.0	12	5	61.2	12	5
2030	**63.0**	18	7	67.8	13	6	72.3	9	4	64.6	18	7	**62.9**	18	7
2040	**63.0**	23	9	70.8	16	7	79.0	10	4	**65.4**	23	9	62.8	24	9
2050	61.3	31	11	**72.3**	20	7	85.3	11	4	64.6	32	11	61.1	31	11
2060	58.4	40	13	72.0	23	9	90.6	13	5	62.5	41	13	58.1	40	13
2070	54.5	48	16	70.2	27	10	95.0	13	5	59.2	50	16	54.1	48	16
2080	49.9	54	18	67.4	32	11	99.0	14	5	55.4	57	17	49.5	54	18
2090	44.8	59	20	63.8	37	12	102.8	15	6	51.4	63	20	44.4	59	20
2100	39.6	64	22	59.8	41	13	**106.6**	17	6	47.6	69	22	39.2	64	22

[a] Human population, in millions.
[b] Percentage of population urbanized.
[c] Percentage of tiger range area urbanized.

2. Methods

2.1. Shared socioeconomic pathways (SSPs)

Five shared socioeconomic pathways (SSPs 1–5) were developed to support the representative concentration pathways (RCPs) used in climate change modelling (O'Neill et al., 2017). RCPs describe a set of alternative trajectories for the atmospheric concentration of key greenhouse gases in a consistent way (O'Neill et al., 2010). The SSP models explain and expand on RCPs by describing alternative pathways of future societal development that lead to different emission trajectories, based on variations of demographic, economic, technological, social, governance, and environmental factors. We summarize the SSPs briefly below; fuller descriptions can be found in O'Neill et al. (2017), KC and Lutz (2017), and Jones and O'Neill (2016) and online at tntcat.iiasa.ac.at/SspDb. It is important to note that these scenarios are meant for heuristic purposes and are not predictions of what will happen, but rather to help society make choices about what kind of future would be preferable.

SSP1: Sustainability: This narrative is based on the concept of sustainability for people and nature, with a high investment in green infrastructure and technology, coupled with low energy demand. Education and health care are priorities, and urbanization is well-managed to be compact.

SSP2: Business as usual: This narrative describes a status-quo scenario in which social, economic, and technological trends follow historical patterns. Technology is assumed to advance steadily along with moderate economic growth.

SSP3: Regional rivalry: This narrative describes countries focused more on domestic or regional interests with an aversion to international relations, as security and competitiveness become predominant issues. This scenario assumes that population growth in poor and rich countries follows divergent paths, and urbanization is discouraged and poorly managed, leading to sprawl.

SSP4: Inequality: This narrative describes a continuing trend toward inequality, whereby populations, both within and between countries, are split between generally wealthy and well-educated groups that support capital-driven sectors on a global scale, and less educated, low-income societies, that provide natural resources to the global economy. Urbanization occurs, but leads to cities segregated by wealth.

SSP5: Fossil-fueled development: This narrative suggests a pathway of development predominantly driven by fossil fuel dependence. Technological advances and education rates are high. Rates of urbanization are high but lead to extensive sprawl.

KC and Lutz (2017) developed demographic projections for countries by translating the SSP scenarios into modifications of fertility, mortality, and immigration patterns for groups of high-fertility and low-fertility countries at decadal intervals from 2000 to 2100. Low-fertility (total fertility rate ≤ 2.9) countries were further separated into rich-OECD countries (based on membership in the Organization for Economic Co-operation and Development and World Bank categorization as “high-income”) and poorer ones. High-fertility countries, which currently or historically had tiger populations, include Afghanistan, Laos, Nepal, and Tajikistan. Low-fertility countries include all the rest: Armenia, Azerbaijan, Bangladesh, Bhutan, Cambodia, China, Democratic People's Republic of Korea (i.e. North Korea), India, Indonesia, Iran, Kazakhstan, Malaysia, Myanmar, Russian Federation, Thailand, Turkey, Turkmenistan, Uzbekistan, and Vietnam. No rich-OECD countries contain TCLs or SSs yet.

The SSP population scenarios have been projected into spatially explicit global raster datasets by Jones and O'Neill (2016), at one-eighth degree (7.5 arc-minutes). A gravity-based downscaling model allocates the forecasted populations based on SSP-specific patterns of urban land-use and spatial development patterns. Year 2000 starting points are based on the gridded population of the world dataset (GPWv3; CIESIN, 2005), where urban population is classified using the Global Rural-Urban Mapping Project urban polygons (GRUMP; Balk et al., 2006), adjusted so that the percentage of urban population matches United Nation-reported values (United Nations - Department of Economic and Social Affairs - Population Division, 2015) for each country of the world. Urban and rural populations are classified at 2.5″ resolution, then aggregated to 7.5″ to apply the model. As such, grid cells may contain both urban and rural populations. Human settlements of at least 5000 persons that were also detected by night-time lights were considered urban (Balk et al., 2005).

2.2. Tiger conservation landscapes (TCLs) and source sites (SS)

A TCL is defined as a block or cluster of blocks of ‘potential effective habitat’ within 4 km of each other, meeting a minimum habitat-specific size threshold, where tigers were confirmed to have occurred between 1997 and 2005 and were not known to have been extirpated since the last observation (Sanderson et al., 2006). Each TCL is named, mapped, and prioritized within biogeographic units representing different tiger ecologies (Dinerstein et al., 2007). For the purposes of this study, the combined area of the 76 TCLs is considered current tiger range (Tables 1, 2).

A SS is defined as an area with breeding tigers, large enough to contain > 25 breeding female tigers, embedded in a larger landscape with the potential to contain > 50 breeding females, and where there is

Table 2
Minimum and maximum scenarios of human population in selected tiger conservation landscapes. Full details are shown in Appendix A.

Tiger conservation landscape	Maximum population scenario				Minimum population scenario				Ratio	
	Dec[a]	SSP[b]	Pop[c]	Urb[d]	Dec[a]	SSP[b]	Pop[c]	Urb[d]	Total[e]	Rural[f]
Russian Far East - China	2000	–	1325	9	2100	4	487	32	2.7	3.6
Corbett - Sonanadi	2100	3	4245	7	2100	5	1596	82	2.7	13.5
Northern Forest Complex - Namdapha - Royal Manas	2100	3	10,608	12	2100	5	3952	70	2.7	7.8
Kaziranga - Garampani	2100	3	2304	6	2100	5	836	54	2.8	5.6
Pachmarhi - Satpura - Bori	2100	3	1580	3	2100	5	550	41	2.9	4.7
Kanha – Phen	2100	3	3209	0	2100	5	1129	18	2.8	3.4
Melghat	2100	3	413	1	2100	1	135	6	3.1	3.2
Pench	2100	3	859	3	2100	5	299	30	2.9	4.0
Simlipal	2100	3	671	0	2100	5	176	52	3.8	8.0
Tadoba Andhari	2100	3	1909	1	2100	5	682	66	2.8	8.2
Sundarbans	2100	3	1616	2	2100	5	507	15	3.2	3.7
Tenasserims	2040	3	5127	4	2100	4	1764	44	2.9	5.0
Western Ghats - Bandipur - Khudrenukh – Bhadra	2100	3	13,473	33	2100	5	4855	82	2.8	10.5
Thap Lan - Pang Sida	2030	3	288	0	2100	4	63	20	4.6	5.8
Taman Negara - Belum	2100	3	6097	63	2000	1	2249	29	2.7	1.4
Bukit Tigapuluh	2050	3	226	0	2100	4	75	13	3.0	3.5
Kerinci Seblat	2050	3	1676	4	2100	4	480	43	3.5	5.9

[a] Decade when maximum/minimum human population is reached.
[b] Shared socioeconomic pathway, see text.
[c] Human population, in thousands.
[d] Population urbanized, percentage.
[e] Ratio of maximum to minimum for total population based on SSP analysis.
[f] Ratio of maximum to minimum for rural population based on SSP analysis.

an existing conservation infrastructure and a legal mandate for protection (Walston et al., 2010). Some of the 42 SSs have multiple, disjunct parts; these data were analyzed separately, leading to analysis of 49 SS areas (Table 3).

2.3. Spatial analysis

All spatial data was projected into a Lambert Equal Area Azimuthal projection, with the central meridian at 110° E and latitude of origin set to 30° N, the same coordinate system as for the TCL analysis (Sanderson et al., 2006). This projection was selected so area calculations could be made and compared across the relatively large geographic extent of the tiger range, which spans the eastern half of Asia.

For each of the 76 TCLs and for the 49 SS areas we extracted total, rural and urban population values for each decade between 2000 and 2100 for each SSP (1–5) by summing across coincident cells from the population grids made by Jones and O'Neill (2016). For each TCL and SS we identified which SSPs lead to minimum and maximum population and the decade at which these low and high demographic events occur (Table 2, SI). The summarized tabular data was then used to create time series figures for all TCLs and SSs (Fig. 2, SI). We also summarized urban populations and area on a percentage basis (Tables 1, 2). To estimate the spatial extent of urban areas, we used any SSP grid cells with non-zero urban populations. Because of the coarseness of the grid, estimated urbanized area should be considered maximum estimates of potential urban land cover (i.e. not all areas within a given cell will be built and paved).

Finally we analyzed the data looking for thresholds of human population density below which tigers become more likely to be found. To estimate these thresholds, we calculated frequency distributions of human population density in 2010 from SSP2 across the four bioregions where tigers were found: Indian subcontinent, Indochina, Southeast Asia, and the Russian Far East and northeastern China. Within each bioregion, we also calculated the frequency distribution of human population density within and outside of the TCLs, assuming the TCLs represent areas where tigers could possibly occur. We normalized each of these distributions (three per bioregion: overall, within TCLs, and outside TCLs) on a percentage basis for comparison. By subtracting normalized distributions within and outside of TCLs from the overall distribution for each bioregion we generate plots of deviation by density (Fig. 3). Negative deviations suggest that those density levels have less likelihood of having tigers than would be expected by random draw; positive deviations suggest greater likelihood than random. As human population densities *within TCLs* increase, we expect deviations to pass from positive to negative; similarly, as densities increase *outside TCLs*, we expect deviations to pass from negative to positive deviations. At these crossing points, we identify thresholds of human population density below which tigers are more likely to occur (see dotted lines, Fig. 3). We then compared these thresholds to decadal SSP estimates of population density for the TCLs within each bioregion to identify when we can expect human population densities to drop below the threshold where tigers become more likely (Fig. 4.) As describe below, we interpret these times as the decades when tigers will become less conservation reliant.

Analysis was conducted using Python with ArcPy and Matplotlib; maps were prepared using ArcGIS 10.6. (ESRI, 2018).

3. Results

3.1. Projected human population scenarios across tiger range

At the beginning of the new millennium in 2000, an estimated 51.1 million people (or approximately 1.4% of the population of Asia) lived in tiger range along with approximately ~4500 tigers, for a ratio approximately 11,355 people to each wild tiger (Fig. 1, Table 1).

From that starting point, the five SSPs diverge in their population projections (Fig. 2). All five pathways suggest increases in the human population for some part of the 21st century. But four of the five suggest peaking around mid-century followed by decreases in human populations sympatric with tigers before 2100. SSP 5 would lead to the earliest peak with 62.9 million in 2030, approximately a decade from now (SSP1 is very similar at 63 million between 2030 and 2040). In contrast analysis of SSP3 predicts the highest population, 106.1 million in 2100. Other SSPs between those extremes predict a peak population of 65.4 million in 2040 for SSP4, and 72.3 million in 2050 for SSP2. By century's end, the pathways are most divergent, with projected populations from a low of 39.2 million for SSP5 (or a decrease of 23% from 2010) to a high of 106.1 million for SSP3 (a doubling of the 2010 population).

Table 3
Minimum and maximum scenarios of human population for 49 tiger source sites areas. Full details are shown in Appendix B.

Source site	Country	Maximum population scenario				Minimum population scenario				Max to min ratio	
		Dec[a]	SSP[b]	Pop[c]	Urban[d]	Dec[a]	SSP[b]	Pop[c]	Urban[d]	Total[e]	Rural[f]
Anamalai Tiger Reserve	India	2100	3	341	4	2100	5	86	50	3.94	7.62
Parambikulam Tiger Reserve	India	2100	3	510	10	2100	5	153	88	3.33	24.36
Bandhavgarh National Park	India	2100	3	73	0	2100	1	19	0	3.80	3.80
Bhadra Wildlife Sanctuary	India	2100	3	413	32	2100	5	209	78	1.98	6.17
Biligiri Ranga Swamy Temple extension	India	2100	3	427	0	2100	5	148	71	2.89	9.98
Jim Corbett National Park	India	2100	3	91	0	2100	5	23	0	3.93	3.93
Dudhwa Tiger Reserve	India	2100	3	1282	1	2100	5	407	81	3.15	16.06
Kalakad Mundanthurai Tiger Reserve	India	2100	3	967	27	2100	5	326	91	2.97	24.60
Kanha National Park	India	2100	3	339	0	2100	1	111	0	3.07	3.07
Kaziranga National Park	India	2100	3	54	0	2100	5	14	55	3.86	8.50
Melghat Tiger Reserve	India	2100	3	47	0	2100	5	9	0	5.18	5.18
Bandipur National Park	India	2100	3	377	3	2100	5	105	25	3.60	4.62
Mudumalai National Park	India	2100	3	143	0	2100	5	21	0	6.76	6.76
Nagarahole National Park	India	2100	3	210	0	2100	5	61	71	3.47	11.81
Pench National Park (Madhya Pradesh)	India	2100	3	93	0	2100	5	28	0	3.38	3.38
Pench Tiger Reserve (Maharastra)	India	2100	3	93	0	2100	5	17	0	5.38	5.38
Periyar Tiger Reserve	India	2100	3	323	0	2100	5	78	54	4.15	8.92
Rajaji Tiger Reserve	India	2100	3	799	43	2100	5	286	93	2.79	22.16
Ranthabmore National Park	India	2100	3	194	10	2100	5	67	32	2.89	3.82
Simlipal Naitonal Park	India	2100	3	250	0	2100	5	60	60	4.13	10.38
Tadoba Andhari Tiger Reserve	India	2100	3	356	0	2100	5	122	57	2.92	6.87
Huai Kha Khaeng Wildlife Sanctuary	Thailand	2000	–	51	0	2100	4	7	0	7.59	7.59
Kaeng Krachan National Park	Thailand	2030	3	74	0	2100	4	19	46	3.86	7.15
Kui Buri National Park	Thailand	2030	3	129	0	2100	4	37	8	3.48	3.76
Endau Rompin Johor National Park	Malaysia	2100	3	4	0	2100	4	1	0	3.16	3.16
Endau Rompin Source Site	Malaysia	2100	3	229	16	2100	4	82	64	2.80	6.43
Endau Rompin State Park Pahang	Malaysia	2100	3	13	0	2100	4	5	29	2.95	4.16
Taman Negara (National Park)	Malaysia	2100	3	25	0	2100	4	8	0	3.14	3.14
Belum Forest Reserve	Malaysia	2100	3	2	0	2100	4	1	0	2.76	2.76
Temenggor Forest Reserve	Malaysia	2100	3	19	0	2000	–	6	0	2.92	2.92
Ulu Masen Ecosystem	Indonesia	2050	3	297	0	2100	4	95	62	3.12	8.22
South Aceh Source Site	Indonesia	2050	3	253	0	2100	4	60	17	4.24	5.10
North Kerinci Source Site	Indonesia	2050	3	66	0	2100	4	11	0	5.80	5.80
Central Kerinci Source Site	Indonesia	2050	3	92	0	2100	4	22	47	4.22	7.92
South Kerinci Source Site	Indonesia	2050	3	46	0	2100	4	10	0	4.74	4.74
Bukit Tigapuluh National Park	Indonesia	2050	3	25	0	2100	4	8	0	3.01	3.01
Bukit Balai Rejang Protection Forest	Indonesia	2050	3	50	0	2100	4	15	0	3.29	3.29
Bukit Barisan Selatan National Park	Indonesia	2050	3	64	0	2100	4	16	0	4.06	4.06
Nam Et Phou Louey NPA[1]	Laos	2100	3	119	0	2100	5	41	38	2.89	4.68
Sundarbans Mangrove Forest	Bangladesh/India	2100	3	1609	3	2100	5	484	12	3.33	3.64
Royal Chitwan/Parsa Naitonal Parks	Nepal	2100	3	1003	8	2000	–	337	10	2.98	3.07
Barida National Park	Nepal	2100	3	408	0	2100	5	126	69	3.23	10.57
Suklaphanta Willdife Reserve	Nepal	2100	3	506	6	2000	–	128	12	3.95	4.23
Sikhote Alinskii Udegeyskaya	Russia	2000	–	3	0	2100	4	1	0	3.85	3.85
Leopardovyi Kedrovaya Pad'	Russia	2000	–	17	0	2100	4	4	24	3.78	4.95
Ussuriiskii	Russia	2000	–	2	0	2100	4	1	24	3.92	5.18
Lazovskii Zov Tigra	Russia	2000	–	5	0	2100	4	1	0	4.20	4.20
Anyuiskii	Russia	2000	–	2	0	2100	4	0	0	4.39	4.39
Botchinskii	Russia	2000	–	3	0	2100	4	1	0	4.10	4.10

[a] Decade when maximum/minimum human population is reached.
[b] Shared socioeconomic pathway, see text.
[c] Human population, in thousands.
[d] Population urbanized, percentage.
[e] Ratio of maximum to minimum for total population based on SSP analysis.
[f] Ratio of maximum to minimum for rural population based on SSP analysis.
[1] Tigers appear to have been extirpated from Nam Et Phou Louey National Protected Area, Laos.

Notably three of the five pathways suggest the year 2100 population may be less than the year 2000 population; SSPs 1 and 5 suggest potential decreases of nearly 20 million people in tiger range over (approximately) the next 80 years.

All five SSPs suggest that the level of urbanization within tiger range will increase during the 21st century. In 2000, the estimated percentage of the population living in towns and cities, after adjustments to conform to the United Nations reported figures, was estimated at approximately 11%, meaning 89% of the sympatric human population in tiger range was rural. By century's end the most urbanized population (derived from SSP4) suggests that 69% of the human population within the current TCLs will live in towns and cities (SSPs 1 and 5 follow similar trajectories and have similar outcomes at ~64% urban). SSP3 leads to the least urbanized population within TCLs, only 17%, suggesting that the socio-economic policies of SSP3 could lead to a near doubling of the rural population in areas important for tigers, from an estimated 45.5 million people in 2000 to 88.8 million people in 2100. SSP2 suggests a moderate level of future urbanization, to 41% by 2100.

All five SSPs suggest the area containing urban settlements (i.e., the area of all grid cells containing urban population) will expand over the next 80 years (Table 1). Analysis of SSPs 1, 4, and 5 indicated that the area of urban settlements will expand from 3% of tiger range to 22% of tiger range by century's end, a seven-fold increase, though the form of that urban development would be quite different. By definition, SSP1

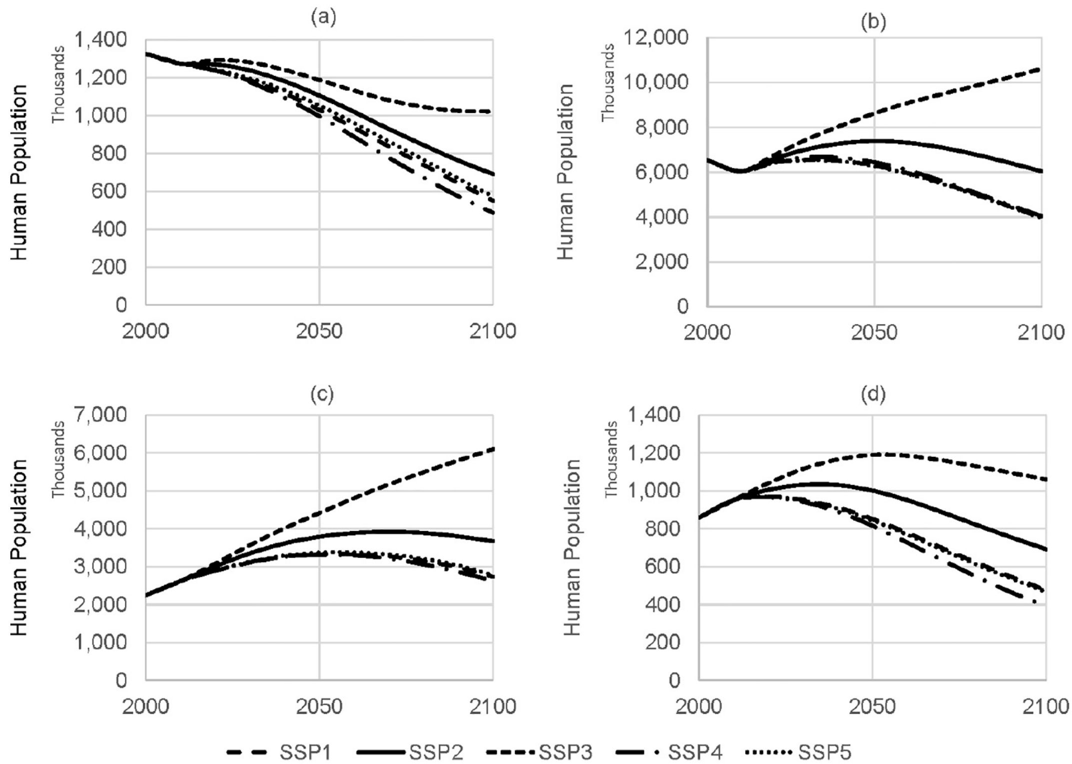

Fig. 2. Comparison of possible future population trajectories for four representative tiger conservation landscapes (TCLs): (a) Russian Far East - Northern China, (b) Northern Forest Complex - Namdapha - Royal Manas, in Myanmar and India, (c) Taman Negara – Belum, Malaysia, and (d) Gunung Leuser, Indonesia. Similar plots for all 76 TCLs (Sanderson et al., 2006) and 49 Source Site areas (sensu Walston et al., 2010) can be found on-line (Appendices A and B, respectively).

would lead to a denser, more compact urban pattern. In contrast, cities and towns in SSP 4, and particularly, SSP5, would be more widely distributed, at lower densities (leading to "urban sprawl", see discussion in Angel et al., 2012). SSP4 would also lead to greater differentiation between wealthier and poorer urban areas relative to the other two scenarios. SSP3 has the smallest expansion, only to 6% (or an approximate doubling in urban area compared to 2010), although within that space we can expect a poorly planned, somewhat fragmented, landscape, resulting from poor land use controls assumed by the scenario. SSP2 has an intermediate value, of 13% of tiger range containing urban development by 2100.

The SSPs suggest that the total size of the urban population within TCLs will continue to grow in the 21st century (Table 1). SSPs 1 and 5 suggest a peaking of urban population around 26.8 and 26.6 million people in the 2080s, respectively, followed by modest declines by 2100. All other SSPs suggest rising urban populations through century's end.

3.2. Projected human population scenarios within TCLs and SSs

For 75 of the 76 TCLs (99%), the highest human population in 2100 is predicted to be obtained from SSP3 (Table 2). The only exception is the Russian Far East – Northeast China TCL, where the highest population is the initial population in 2000 (all SSPs predict 21st century declines in population in that area). The pathways that obtain the lowest populations vary among TCLs: for 37 TCLs, SSP5 yields the lowest population; 25 for SSP4; and 14 for SSP1 (Table 2). In no case does SSP2 yield the highest or the lowest population for any TCL, not surprising given that this is the "middle of the road" scenario. On average, the ratio of maximum to minimum total human population predictions in the TCLs is 3.15, suggesting that socio-economic policies could swing the human population some three-fold between minimum and maximum scenarios. The ratio is even larger for rural populations; the average ratio maximum to minimum is 6.19:1, though there is considerable variation among TCLs (Table 2). For example, in the Corbett-Sonanadi tiger landscape in India, the ratio between the highest rural population of SSP3 and the lowest rural population of SSP5 (both in 2100) is 13.5:1. For the Shendurney tiger landscape in Kerala State in India the ratio is 29.1:1 comparing 2100 scenarios. In such extreme cases, the differences are created both by lower population growth rates and higher urbanization levels leading to large differences in rural population in and surrounding TCLs.

For 42 of the 49 SS areas (86%), SSP3 generates the largest human populations over the course of the 21st century (Table 3), a result of the higher fertility rates and larger rural populations associated with SSP3. For the remaining 7 areas, the highest population is the starting population in 2000, meaning all SSPs suggest declining human populations going forward, though even in these cases, SSP3 leads to highest human populations. The decade of the largest population varies by SS. For 32 SS areas, the highest populations are predicted to be observed in 2100; for 8, in 2050; and for 2, in 2030. In other words, for 35% of SSs, even following the fastest growing pathway, the human population is predicted to peak and decline before century's end.

For SSs areas, minimum populations vary by SSP (Table 3). For 22 SS areas, SSP5 yields the smallest sympatric human population; for a different set of 22 sites, SSP4, and for 2 sites, SSP1. SSP2 and SSP3 in no case lead to lowest populations in SSs. For 94% of the SSs, the lowest predicted human population is not obtained until 2100.

3.3. Population density thresholds for tiger conservation landscapes

We found that the population density thresholds derived from analysis of areas inside and outside of TCLs vary between bioregions (Fig. 3). The apparent density thresholds, in terms of persons per square kilometer, were found to be: 140 or less for the Indian subcontinent; 30 or less for Indochina; 20 or less for Southeast Asia; and 10 or less for the Russian Far East. Because tigers persist in some areas that are above these thresholds currently (e.g. western Ghats and Terai Arc in the Indian subcontinent, Taman Negara in Malaysia) and do not persist in

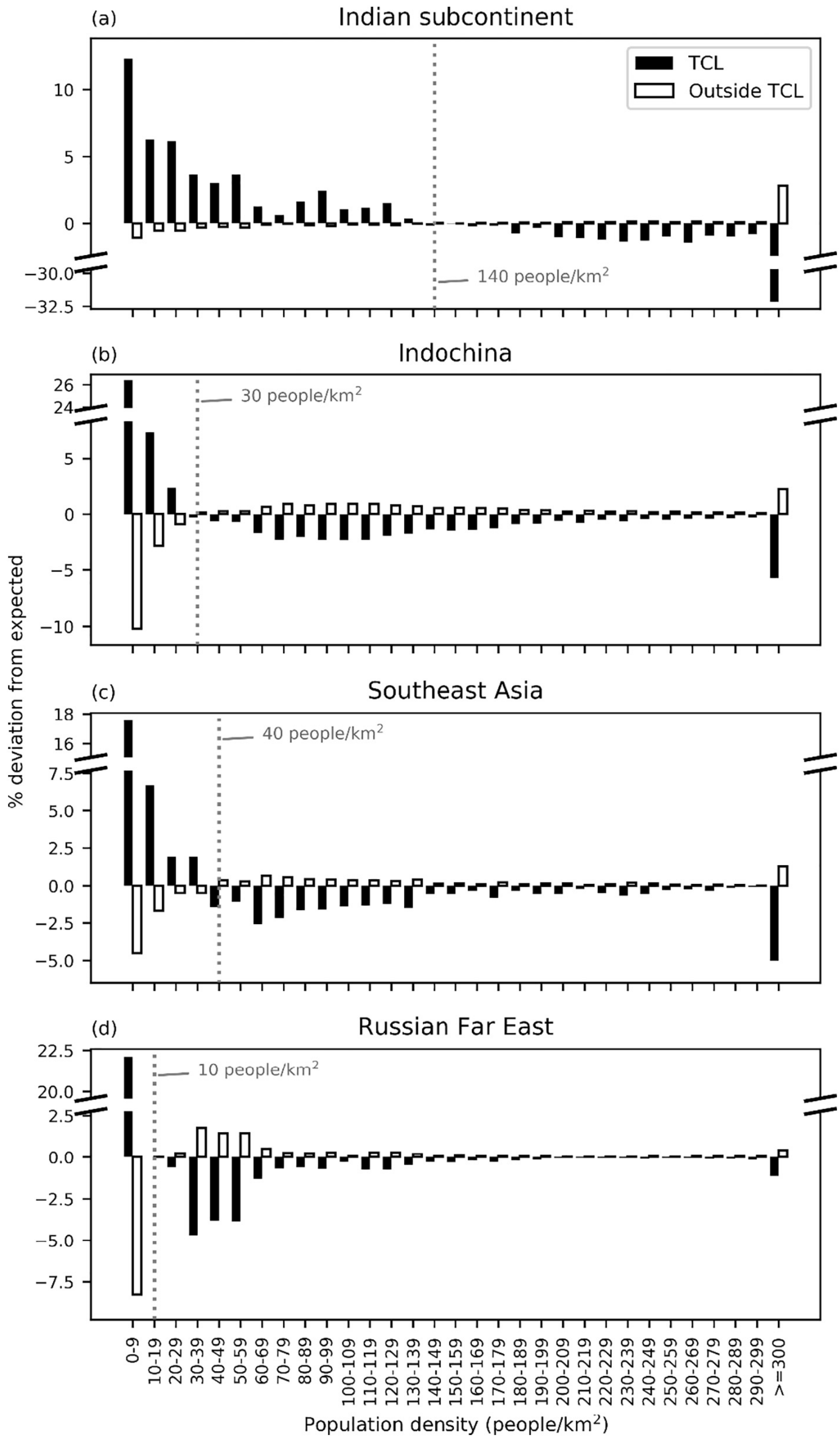

Fig. 3. Deviations of frequency distribution of human population densities inside and outside of TCLs compared to the overall distribution of population density for four bioregions [(a) Indian subcontinent, (b) Indochina, (c) Southeast Asia (consisting of peninsular Malaysia and Sumatra), and (4) Russian Far East and northern China] reveal different population density thresholds, as indicated by dotted lines.

areas below the population thresholds (for example, the Northern Plains of Cambodia), we interpret these thresholds as indicative of population levels where high levels of conservation effort are warranted, not as the levels where tigers will inevitably be extirpated. Similarly some conservation efforts will still be required (for example, warding against poaching) at low population densities. We compared these threshold levels to the population density predictions for each SSP for each TCL, to give some rough measure of the period of intensive conservation dependence for tigers in different parts of the range (Fig. 4). These analyses suggest that trajectory of future population is

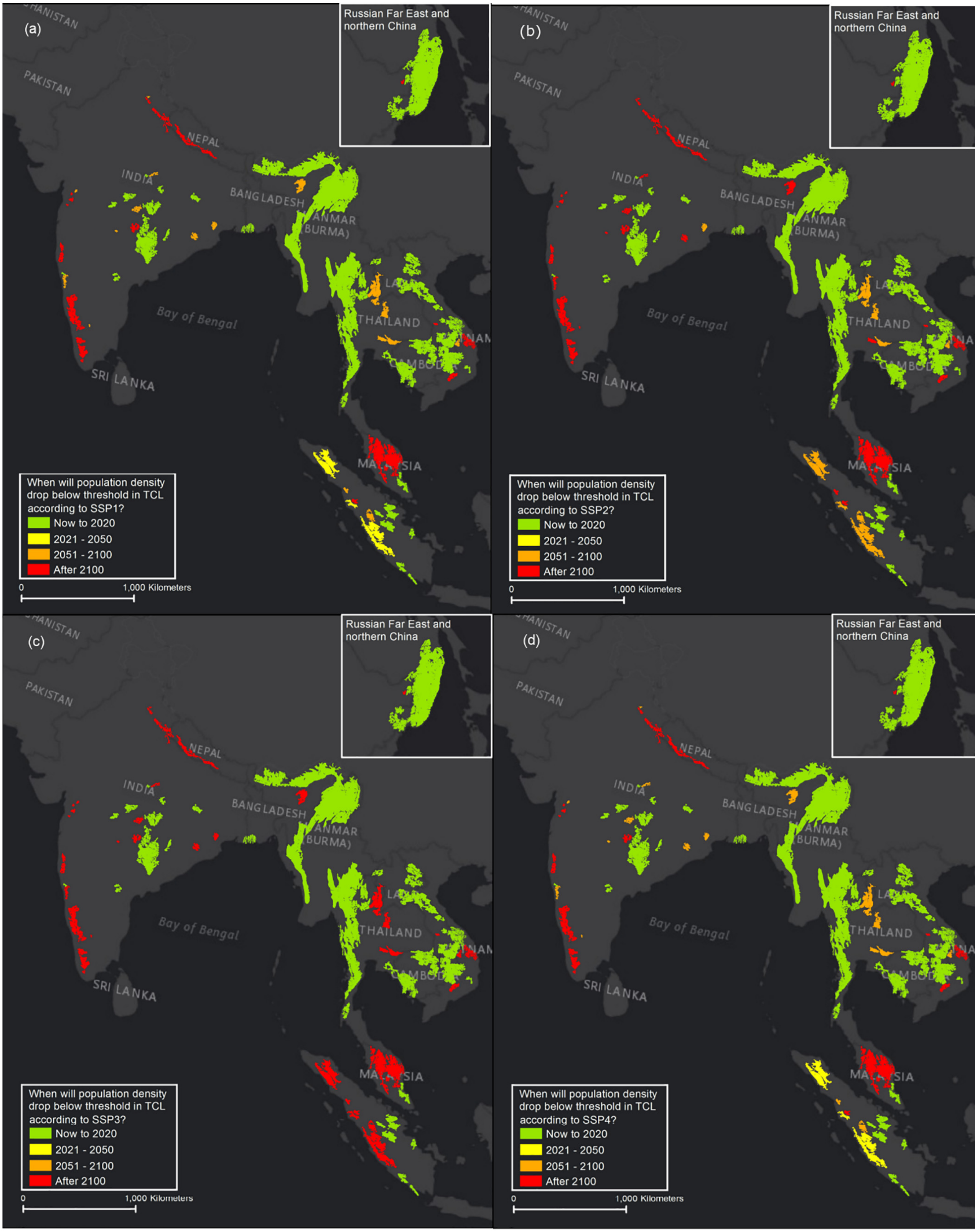

Fig. 4. Maps of the tiger conservation landscapes (TCLs) colored to shown when human population densities are anticipated to drop below the population density thresholds shown on Fig. 3, for (a) SSP1, (b) SSP2, (c) SSP3, and (d) SSP4. Note that the results for SSP5 are identical with those for SSP4.

most important for Sumatra and some of the smaller TCLs in Indochina and the Indian subcontinent, but the overall pattern is surprisingly not so different among the various SSPs.

4. Discussion

Tigers are a conservation-reliant species (Scott et al., 2010). This study suggests that tiger populations will continue to be conservation-reliant through most of the 21st century as well, though how much conservation effort, and what kinds of effort, will likely change as the demographic transition proceeds in Asia (Choe, 2017).

The SSPs help us glimpse possible future histories of tiger conservation, while keep in mind they are mainly of heuristic value; not so much predictions of what will happen, but rather a way of thinking about what could happen. The analysis of tiger range as a whole suggests that while human pressures will persist, and may indeed rise for some decades (see Bradshaw and Brook, 2014), eventually population will peak and lead to decreases in human population in areas important for tigers, as people in Asia continue their historically unprecedented movements from rural areas to towns and cities. Those decreases could be quite large, such as with SSP1, which predicts a peak in population in the 2030–2040 time period, and an absolute drop in human population of 17.6 million people in tiger range by 2100, a 35% drop (Table 1). In contrast, the future suggested by SSP3, where both total and rural populations grow (by 49.2 million and 40.8 million, respectively), is likely to lead to even higher pressures on tigers and their prey and habitat, and therefore dramatically increased costs for conservation through century's end. Similar observations can be made about individual TCLs and SSs (Tables 2, 3; Appendices A, B), where SSP3 leads in nearly all cases to the highest sympatric human population, and the pro-urbanization scenarios (SSPs 1,4,5) lead to lower in total, and less rural, populations. Making cities work can be seen as not only a benefit to the people who live in those cities, but a benefit to tigers as well.

Urban development can take on many different forms, most of which are not well captured by this analysis, and will require further work to clarify at the scale of individual TCLs. The cell resolution of the Jones and O'Neill (2016) projections mean that the urban areas reported here should be considered maximum extents that need further refinement with locally appropriate data or proxies (e.g. Leyk et al., 2018). Such analysis could help better distinguish the effects on tigers (and other wildlife) of SSPs 1, 4, and 5 from urban development, expansion of road networks, and changes in land use. Generally speaking rapid urbanization without planning for transportation and land use can lead to sprawling settlements, fragmenting tiger habitat, increasing conflict, and decreasing suitability for tigers and their prey (per SSP 4), while increasing dependence on fossil fuels can also drive an increase in roads, leading to greater barriers to tiger movement (per SSP 5). We know that urban expansion can have significant effects on species and ecosystems (Grimm et al., 2008; Güneralp and Seto, 2013), which is why it is necessary that urban planning include the needs of wildlife, both directly in urban plans (e.g. Hess et al., 2014) and indirectly, as through studies like this one. Planning with sustainability in mind (e.g. SSP 1; Roberts and Kanaley, 2006) could lead to more concentrated urban areas, less landscape fragmentation, fewer carbon emissions (O'Neill et al., 2010), and presumably better long-term outcomes for people and tigers.

The land use effects of urbanization may be particularly important in those TCLs for which biome-specific population density thresholds identified on Fig. 3 will not be reached in the 21st century (the red-colored areas on Fig. 4). Such areas include the Eastern and Western Ghats in India, the Terai Arc of India and Nepal, and Peninsular Malaysia, among others. For these TCLs, tigers will remain conservation-reliant and may experience, more than in other localities, the negative effects of habitat lost to urban areas. In other cases, lower trajectories of demographic growth will have benefits for TCLs closer to populated areas, and particularly, on the island of Sumatra, as shown by comparing SSPs on Fig. 4.

The biome-specific population density thresholds, distinguishing where tigers are and are not found (Fig. 3), demonstrate the great differences in tiger conservation between the Indian subcontinent and other bioregions. This measure suggests that tigers on the Indian subcontinent can live with human population densities an order of magnitude higher than in any other part of the range (140 persons/km^2 compared to 10–30 persons/km^2; contrast also with the implicit < 1 person/km^2 threshold in most of China, see Kang et al., 2010). This result seems consistent with recent studies of human tolerance of wildlife in India (e.g. Karanth et al., 2017), but warrants further investigation in terms of the ecosystem and cultural factors at play. It also suggests that by changing cultural factors in other regions, new forms of compatibility between human life and tiger existence might be developed.

That said lower sympatric human population densities on their own are not the only answer. Even a few people actively hunting tigers can extirpate a population of tigers, so continued protection efforts will be necessary, even as the demographic transition and urbanization changes the where and how people live over coming decades. Fig. 4 shows that there are TCLs today where human population densities are low enough to allow tigers, but nonetheless tigers have been extirpated (e.g. Northern Plains of Cambodia.)

On a related theme, it is unclear how the on-going of urbanization of Asia will influence consumption patterns and therefore changes in natural resource use in tiger landscapes. Generally speaking as people move to cities and gain more income, consumption patterns do change (Delgado, 2003; United Nations - Economic and Social Commission for Asia and the Pacific, 2017; Sanderson et al., 2018), but further research is required to trace how changing consumption results in changes in the kinds and localities of natural resource extraction.

Because of the demographic, geographic, and consumptive effects of urbanization, as partially revealed by analysis of the SSPs, it is clear that cities matter for tigers. Our findings are consistent with the "Bottleneck and Breakthrough" theory described by Sanderson et al. (2018), which posits that urbanization will drive economic and demographic changes that have tremendous importance for the practice of global conservation. For tigers, the breakthrough could come as early as 2030–2040 (i.e. as soon as two decades from now, within the career of a young tiger conservationist), or not until the next century (the great-grandchildren of today's conservationists). Urbanization is linked with lower human mortality and fertility levels that result from a constellation of factors: increased parental investment in children, better economic and education opportunities, enhanced rights for women, and improved healthcare (Rammohan, 2004; Choe, 2017; Lutz and KC, 2017). Given good governance, health, and safety – circumstances which are not universally found in Asian towns and cities today (c.f. Sheng, 2010) – people working in urban areas also generate new ideas, rapidly innovate and iterate, and have the capital and interconnectivity to deploy improvements widely (Nicholls, 2008; Glaeser, 2011).

Therefore tiger conservation will benefit from coupling in situ protection with improved governance, education efforts, and conservation constituency building in Asia's burgeoning towns and cities. These efforts probably require partnerships between more rural-focused conservation organizations, within and without government, with urban-focused organizations, governmental and non-governmental, seeking to improve the welfare, planning, and environmental effects of Asia's growing cities (Angel, 2012). Towns and cities, with an expanding middle class (Montgomery and Balk, 2017), increasingly working in service rather than manufacturing or natural resource extraction industries (United Nations - Economic and Social Commission for Asia and the Pacific, 2017), offer new opportunities to mobilize powerful national constituencies for tiger conservation in Asia. Such movements are essential not only to support and finance essential 21st century tiger conservation efforts, but also to diminish threats that emanate from land and resource consumption patterns of increasingly wealthy urbanites through regulatory or economic policy (for some examples, see Kalkuhl et al., 2018; Wang et al., 2018).

Finally we note that our approach to linking human demography and wildlife conservation is not restricted to tigers. Any species that ranges across wide areas could be subject to a similar analysis using the SSP framework and the spatial population projections from Jones and O'Neill (2016). Such analysis enables conservation biologists to connect specific geographies and threats to urban, national, and international policies, especially when and where threats are driven by human population and/or distinguishable between rural and urban lifestyles.

5. Conclusions

Urbanization and the subsequent human demographic transition is arguably the most important historical trend shaping the future of conservation (Sanderson et al., 2018). How that transition plays out is not pre-determined. Rather it depends on the policy decisions that governments, and the societies they represent, take with respect to fundamental matters such as urban governance, education, economic reform, and the movement of people and trade goods (O'Neill et al., 2017). Such matters have not traditionally been seen as part of the conservation practice, but increasingly they must be if we want a world with tigers, forests, and wildness, to persist beyond the 21st century.

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Competing interests

The authors have not competing interests to declare.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2018.12.017.

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