

LJMU Research Online

Santika, T, Sherman, J, Voigt, M, Ancrenaz, M, Wich, S and Meijaard, E

Effectiveness of 20 years of conservation investments in protecting orangutans

<http://researchonline.ljmu.ac.uk/id/eprint/16384/>

Article

Citation (please note it is advisable to refer to the publisher's version if you intend to cite from this work)

Santika, T, Sherman, J, Voigt, M, Ancrenaz, M, Wich, S and Meijaard, E
Effectiveness of 20 years of conservation investments in protecting orangutans. Current Biology. ISSN 0960-9822 (Accepted)

LJMU has developed **LJMU Research Online** for users to access the research output of the University more effectively. Copyright © and Moral Rights for the papers on this site are retained by the individual authors and/or other copyright owners. Users may download and/or print one copy of any article(s) in LJMU Research Online to facilitate their private study or for non-commercial research. You may not engage in further distribution of the material or use it for any profit-making activities or any commercial gain.

The version presented here may differ from the published version or from the version of the record. Please see the repository URL above for details on accessing the published version and note that access may require a subscription.

For more information please contact researchonline@ljmu.ac.uk

<http://researchonline.ljmu.ac.uk/>

Effectiveness of 20 years of conservation investments in protecting orangutans

Authors

Truly Santika^{1,53}, Julie Sherman², Maria Voigt³, Marc Ancrenaz^{4,5}, Serge A. Wich⁶, Kerrie A. Wilson⁷, Hugh Possingham⁸, Emily Massingham⁸, Dave J.I. Seaman³, Alison M. Ashbury^{9, 10, 11}, Taufiq S. Azvi^{12, 13}, Graham L. Banes¹⁴, Elizabeth J. Barrow¹⁵, David F.R.P. Burslem¹⁶, Robert A. Delgado¹⁷, Andi Erman¹⁸, Gabriella Fredriksson¹⁹, Benoit Goossens^{20, 21, 22}, Max Houghton²³, Tito P. Indrawan²⁴, Ricko L. Jaya²⁵, Tomoko Kanamori²⁶, Cheryl D. Knott^{27, 28, 15}, Ashley Leiman²⁹, Darmawan Liswanto^{30, 31}, Martin Mach³², Andrew J. Marshall³³, Julien G.A. Martin³⁴, Lelyana Midora², Adam Miller³⁵, Sol Milne¹⁶, Courtney Morgans³, Nardiyono³⁶, Dyah Perwitasari-Farajallah^{37, 38}, Dolly Priatna^{39, 40}, Robert Risch⁴, Galuh M. Riyadi^{42, 43}, Anne Russon⁴⁴, Juhardi Sembiring⁴⁵, Endro Setiawan⁴⁶, Mohammad Sidiq⁴², Donna Simon⁴⁷, Stephanie Spehar⁴⁸, Matthew J. Struebig³, Ibrahim Sumardi⁴⁶, Albertus Tjiu⁴⁹, Rizki Wahyudi^{46, 52†}, Achmad Yanuar⁵⁰ & Erik Meijaard^{3, 5, 8, 51*}

Affiliations

¹ Natural Resources Institute (NRI), University of Greenwich, Central Avenue, Chatham Maritime, Kent, ME4 4TB, UK

² Wildlife Impact, P.O. Box 31062, Portland, OR 97231, USA

³ Durrell Institute of Conservation and Ecology, School of Anthropology and Conservation, Marlowe Building, University of Kent, Canterbury, Kent CT2 7NR

⁴ HUTAN – KOCP, P.O. Box 17793, 88874 Kota Kinabalu, Sabah, Malaysia

⁵ Borneo Futures, 8th Floor, PGGMB Building, Jalan Kianggeh, Bandar Seri Begawan, BS8111, Brunei Darussalam

- 23 ⁶ School of Biological and Environmental Sciences, Tom Reilly Building, Byrom Street, Liverpool John
24 Moores University, Liverpool L3 3AF, UK
- 25 ⁷ Queensland University of Technology, 2 George St, Brisbane, Queensland 4000, Australia
- 26 ⁸ UQ International, Level 2, JD Story building, St Lucia campus, The University of Queensland,
27 Brisbane, Queensland 4072, Australia
- 28 ⁹ Laboratory for Zoology and Evolutionary Biology, Department of Biology - Fach 618, University of
29 Konstanz - Universitätsstraße 10, D-78457 Konstanz, Germany
- 30 ¹⁰ Department for the Ecology of Animal Societies, Max Planck Institute for Animal Behavior,
31 Universitätsstraße 10, D-78464 Konstanz, Germany
- 32 ¹¹ Department of Anthropology, Rämistrasse 71, 8006, University of Zurich, Zurich, Switzerland
- 33 ¹² Universitas Nahdlatul Ulama Sumatera Utara, Jl. Gaperta Ujung No.2, Tj. Gusta, Kec. Medan
34 Helvetia, Kota Medan, Sumatera Utara 20125, Indonesia
- 35 ¹³ Pesona Tropis Alam Indonesia (PETAI), Komplek Tasbi 2, Jl. Ring Road Blk. V No.21, A M P L A S,
36 Kec. Medan Amplas, Kota Medan, Sumatera Utara 20122, Indonesia
- 37 ¹⁴ Wisconsin National Primate Research Center, University of Wisconsin–Madison, Southwest
38 Commuter Path, Madison, WI 53715, United States
- 39 ¹⁵ Gunung Palung Orangutan Conservation Program, P.O. Box G 1661 Massachusetts Ave Lexington,
40 MA 02420-2020, United States
- 41 ¹⁶ School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen, Aberdeenshire
42 AB24 2TZ, Scotland, UK
- 43 ¹⁷ U.S. National Science Foundation, 2415 Eisenhower Avenue, Alexandria, Virginia, USA
- 44 ¹⁸ GFA/KWF, Kapuas Hulu Program, Pontianak, West Kalimantan, Indonesia

- 45 ¹⁹ Vocabolo Ca' di Bracco, Via Migianella 381, Loc Molino Vitelli, 06019 Umbertide PG, Italia
- 46 ²⁰ Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma MUIS, Block B 5th Floor, 88100
47 Kota Kinabalu, Sabah, Malaysia
- 48 ²¹ Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Sir Martin
49 Evans Building, Museum Avenue, Cardiff CF10 3 AX, UK
- 50 ²² Sustainable Places Research Institute, Cardiff University, 33 Park Place, Cardiff CF10 3BA, UK
- 51 ²³ Research Centre in Evolutionary Anthropology, and Palaeoecology, School of Natural Sciences and
52 Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3
53 3AF, United Kingdom
- 54 ²⁴ Forum Konservasi Orangutan Kalimantan Barat, Lab 515 Building, 3rd Floor Jl. Salihara No. 41A -
55 Pasar Minggu Jakarta, 12520, Indonesia
- 56 ²⁵ Orangutan Information Centre, Bunga Sedap Malam XVIII C No. 10, Medan Selayang, North Sumatra
57 20131, Indonesia
- 58 ²⁶ Primate Research Institute, Kyoto University, Inuyama, Aichi 484-8506, JAPAN
- 59 ²⁷ Department of Anthropology, Boston University, 232 Bay State Road, Boston, MA 02215, United
60 States
- 61 ²⁸ Department of Biology, Boston University, 5 Cummington Mall, Room 101 Boston, MA 02215,
62 United States
- 63 ²⁹ Orangutan Foundation, 7 Kent Terrace, London NW1 4RP, United Kingdom
- 64 ³⁰ Yayasan Titian Lestari, Jl. Komp. Alex Griya Permai I, Bangka Belitung Darat, Kec. Pontianak
65 Tenggara, Kota Pontianak, Kalimantan Barat 78124, Indonesia

- 66 ³¹ Yayasan SINTAS, Jl. Merdeka Barat No.665, Mariana, Kec. Pontianak Kota, Kota Pontianak,
67 Kalimantan Barat 78243, Indonesia
- 68 ³² Bumitama, Jl. Melawai Raya No.10, RT.3/RW.1, Melawai, Kec. Kby. Baru, Kota Jakarta Selatan,
69 Daerah Khusus Ibukota Jakarta 12160, Indonesia
- 70 ³³ University of Michigan, Department of Anthropology, Department of Ecology and Evolutionary
71 Biology, Program in the Environment, School for Environment and Sustainability, Ann Arbor, MI
72 48109, USA
- 73 ³⁴ Biology Department, University of Ottawa, Gendron Hall, Room 160, 30 Marie Curie, Ottawa, ON
74 Canada K1N 6N5
- 75 ³⁵ Planet Indonesia, Webster Groves, MO 63119, United States
- 76 ³⁶ Austindo Nusantara Jaya, Menara BTPN, 40 Floor, Jl. Dr. Ide Anak Agung Gde Agung, Kav. 5.5-5.6,
77 Kawasan Mega Kuningan, Jakarta 12950, Indonesia
- 78 ³⁷ Department of Biology, Gedung Biologi, Jalan Agatis, Kampus IPB, Dramaga, Bogor 16680,
79 Indonesia
- 80 ³⁸ Primate Research Center, IPB University, Jl. Lodaya II/5, Bogor 16151, Indonesia
- 81 ³⁹ Graduate School of Environmental Management, Pakuan University, Jl. Pakuan, RT.02/RW.06,
82 Tegallega, Kecamatan Bogor Tengah, Kota Bogor, Jawa Barat 16129, Indonesia
- 83 ⁴⁰ Belantara Foundation, Dimo Space, Jl. Timor No.6, RT.9/RW.4, Gondangdia, Kec. Menteng, Kota
84 Jakarta Pusat, Daerah Khusus Ibukota Jakarta 10350, Indonesia
- 85 ⁴¹ Rhino and Forest Fund, Auf dem Stein 2, 77694 Kehl, Germany
- 86 ⁴² Universitas Tanjungpura, Jl. Prof. Dr. H. Prof. Dr. H. Hadari Nawawi, Bansir Laut, Kec.
87 Pontianak Tenggara, Kota Pontianak, Kalimantan Barat 78124, Indonesia

- 88 ⁴³ Malaysian Environmental Consultants, 82 Jalan Ampang Hilir , 55000 Kuala Lumpur, Malaysia.
- 89 ⁴⁴ Glendon College of York University, 2275 Bayview Ave, Toronto M4N 3M6, ON, Canada
- 90 ⁴⁵ Universitas Nahdlatul Ulama Sumatera Utara, Jl. Gaperta Ujung No.2, Tj. Gusta, Kec. Medan
- 91 Helvetia, Kota Medan, Sumatera Utara 20125, Indonesia
- 92 ⁴⁶ Gunung Palung National Park Office, Padu Banjar, Kec. Simpang Hilir, Kabupaten Ketapang,
- 93 Kalimantan Barat 78857, Indonesia
- 94 ⁴⁷ WWF – Malaysia, Suite 1-6-W11 6th Floor, CPS Tower, Centre Point Complex No. 1., Lorong Centre
- 95 Point, Pusat Bandar, 88000 Kota Kinabalu, Sabah, Malaysia
- 96 ⁴⁸ Sustainability Institute for Regional Transformations, 4483 Sage Hall, 835 High Ave., Oshkosh, WI
- 97 54901, USA
- 98 ⁴⁹ World Wide Fund for Nature-Indonesia (Yayasan WWF Indonesia), WWF Indonesia Gedung Graha
- 99 Simatupang, Tower 2, Unit C, 7 Floor, Jl. Letjen TB. Simatupang Kav. 38, Jakarta Selatan 12540,
- 100 Indonesia
- 101 ⁵⁰ Graduate School, Department of Biology, Universitas Nasional, Jl. Sawo Manila, Pejaten Ps., South
- 102 Jakarta 12520, Indonesia
- 103 ⁵¹ Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12844, Prague 2,
- 104 Czech Republic
- 105 ⁵² [†]In Memoriam.
- 106 ⁵³ Lead contact
- 107 * Correspondence: emeijaard@borneofutures.org
- 108 Twitter: @emeijaard

Keywords: biodiversity; conservation finance; evidence-based conservation; great apes; impact assessment; Indonesia; Malaysia; orangutan; Pongo; tropical forest

Summary

Conservation strategies are rarely systematically evaluated, which reduces transparency, hinders the cost-effective deployment of resources, and hides what works best in different contexts ¹. Using data on the iconic and critically endangered orangutan (*Pongo* spp.), we developed a novel spatiotemporal framework for evaluating conservation investments. We show that around USD 1 billion was invested between 2000 and 2019 into orangutan conservation by governments, non-governmental organizations, companies and communities. Broken down by allocation to different conservation strategies, we find that habitat protection, patrolling and public outreach had the greatest return-on-investment for maintaining orangutan populations. Given variability in threats, land-use opportunity costs, and baseline remunerations in different regions, there were differential benefits-per-dollar invested across conservation activities and regions. We show that, while challenging from a data and analysis perspective, it is possible to fully understand the relationships between conservation investments and outcomes, and the external factors that influence these outcomes. Such analyses can provide improved guidance towards more effective biodiversity conservation. Insights into the spatiotemporal interplays between the costs and benefits driving effectiveness can inform decisions about the most suitable orangutan conservation strategies for halting population declines. While our study focuses on the three extant orangutan species of Sumatra and Borneo, our findings have broad application for evidence-based conservation science and practice worldwide ¹.

Introduction

The three orangutan species, *Pongo pygmaeus* in Indonesian and Malaysian Borneo, and *P. abelii* and *P. tapanuliensis* in Sumatra, Indonesia, are in rapid decline²⁻⁵, and there is a global concern about the risk of their extinction in the wild⁶⁻⁸. The main drivers of orangutan decline are the loss and degradation of forest habitat, mostly for agricultural development²⁻⁵, and killing^{9,10}. Over the past 50 years, a diversity of activities has been implemented to reduce and mitigate threats to orangutans^{11,12}. Which activities lead to the best outcome, however, is subject to extensive debate^{13,14}. Furthermore, the species are distributed across four regions (Sumatra and Kalimantan (Indonesia), and the Malaysian states of Sabah and Sarawak) (Figure 1) with differential exposure to threats, heterogeneous biophysical and socioeconomic characteristics, and diverse government policies. As a result, the extent to which the activities and the concomitant funding are benefitting species persistence is unknown, as are the key externalities that shape these benefits¹⁴.

We developed a comprehensive framework to assess the impact of conservation investments in wildlife conservation across spatial and temporal scales. We applied this framework to investments in orangutan conservation activities across Kalimantan, Sabah and Sumatra between 2000 and 2019. We collected data on financial investments from private and public organizations involved in orangutan conservation in these regions. The benefit of a given conservation activity was estimated as the improvement in the predicted orangutan occurrence compared to the counterfactual of no activity. By comparing the spatiotemporally-explicit investments with the estimated benefit, we evaluated the efficiency of two decades of investments in six activities aiming to reduce orangutan population declines: (i) habitat protection and management, (ii) habitat restoration, (iii) patrolling and law enforcement, (iv) rescue and rehabilitation, (v) translocation and reintroduction, and (vi) public outreach and capacity building. The orangutan conservation Theory of Change (ToC) pathways representing the chain of outcomes resulting from the conservation activities are shown in Figures S1 and S2. The estimated investment in research on orangutans and their habitats (excepting those exclusive to orangutan rehabilitation and translocation) was also quantified (Figure S3). Through application of our framework to orangutan conservation, we were able to answer the following: (1) Which conservation activities have been conducted, at what costs, and how were they distributed

spatially? (2) What was the net benefit of each conservation activity? (3) Within the contemporary range of wild orangutan, which activities yielded the greatest return-on-investment, and how did this vary between regions?

Results

Investment in conservation activities for orangutans

In the period between 2000 and 2019, the total nominal investment on orangutan-related conservation activities across Kalimantan, Sumatra, and Sabah was US\$ 870 million. In real value, i.e., the nominal value adjusted for inflation (see Methods), this equates to US\$ 1.16 billion. The annual average of the nominal investment in the period 2015–2019 was US\$67 million, which was a nearly threefold increase compared the annual average of US\$ 26 million from 2000–2005 (Figure 2a). The real value of investment had increased 1.3 times (Figure 2a) and varied by region. Between 2000 and 2019, an average annual operating expenditure valuing \$24–26 million had been allocated in both Kalimantan and Sabah, whereas, in Sumatra, there was an average annual expenditure of \$8 million (Figures 2b and 3). Considering regional differences in available habitat, Sabah had the greatest per unit habitat investment overall, with an average annual operational expenditure of \$676 per km² of orangutan habitat (Figure 2c). Comparatively, Sumatra invested \$272 per km² annually, whereas Kalimantan only invested \$85 per km² annually on average.

The allocation of investments to different conservation activities differed between regions (Figure 4a). In Kalimantan, the largest proportion of the total annual investment was assigned to habitat protection (31%), followed by rescue and rehabilitation (18%) and public outreach (16%). In Sabah, patrolling and law enforcement made up the largest proportion of the total annual expenditure (38%), followed by habitat protection (20%) and outreach programs (15%). In Sumatra, a substantial proportion of the total annual investment was allocated to habitat protection (47%), followed by patrolling (20%) and public outreach (14%).

In Kalimantan, orangutan translocation and reintroduction programs were the most expensive activity (\$427 per km²), while habitat protection was \$252 per km² (Figure 4b). In Sabah, patrolling was the most

expensive activity (\$1,303 per km²), double that of habitat protection. In Sumatra, habitat protection was the most expensive approach (\$734 per km²), double that of patrolling activities. Sabah had the greatest investment in research (\$407 per km² per annum) compared to less than \$150 per km² per annum in Kalimantan and Sumatra.

Benefits of conservation activities for orangutans

Between 2000-2004 and 2015-2019, the mean probability of orangutan occurrence across the wild orangutan contemporary range in Kalimantan, Sumatra and Sabah declined by approximately 20%. Based on our analysis of the relationship between the species' probability of occurrence and density (Figure S4), this translates to an estimated decline from 17.4 to 13.8 (95% confidence interval (CI): from 15.1-19.7 to 11.4-16.2) individuals per 5x5 km² grid-cell on average between 2000 and 2019 for Kalimantan, from 13.9 to 11.4 (95% CI: from 10.6-17.2 to 7.6-15.2) individuals per grid-cell for Sabah, and from 10.3 to 8.7 (95% CI: from 7.9-12.7 to 6.3-11.1) individuals per grid-cell for Sumatra (Figure S4).

The benefit of a conservation activity was estimated by comparing the orangutan occurrence probability (given existing conservation actions) with the counterfactual in the absence of conservation activity. Across the three regions, habitat protection and patrolling were estimated to generate the greatest benefits in maintaining orangutan occurrence (Figure 5a). In Kalimantan, habitat protection and patrolling were associated with an average 13% and 3.6% improvements in the species' occurrence probability per 5x5 km² grid-cell every five years between 2000 and 2019 compared to the counterfactual of no investment in these activities (Figure 5b). In Sabah, habitat protection and patrolling were estimated to improve orangutan occurrence by 8.7% and 12% respectively, whereas in Sumatra they contributed to 16% and 12% improvements in occurrence respectively (Figure 5b). Besides these two conservation activities, public outreach activities generated a large benefit for the orangutan populations in Sabah, providing 7.4% improvement in the occurrence probability compared to the counterfactual of no outreach programs (Figure 5b).

Return-on-investment of orangutan conservation activities

The return-on-investment for a given orangutan conservation activity was estimated as the improvement in the species' occurrence probability compared to the counterfactual in the absence of the activity divided by

the investment cost for that activity. Across Kalimantan, Sabah, and Sumatra and within the orangutan's contemporary range, habitat protection was estimated to generate the highest return-on-investment overall, providing an average 12% improvement in orangutan probability of occurrence per 5×5 km² grid-cell per annual investment of US\$10,000 compared to the counterfactual (Figure 6a). Patrolling activities had moderate benefit-per-dollar, providing a 9.2% improvement in orangutan occurrence probability.

There were variations in the return-on-investment of conservation activities across the different regions (Figure 6b). In Kalimantan, habitat protection had the highest benefit-per-dollar (providing an average improvement of 21% in the orangutans' probability of occurrence per 5×5 km² grid-cell per US\$10,000 annual investment compared to the counterfactual), followed by patrolling (9.4%). This translates to an estimated density benefit of 7.4 orangutans per 25 km² for every annual spending of US\$10,000 for habitat protection, and a density benefit of 3.2 orangutans for patrolling activities. In Sabah, outreach programs had the highest benefit-per-dollar invested (average improvement of 6.1% in occurrence probability per 5×5 km² grid-cell per US\$10,000 annual investment compared to the counterfactual), followed by habitat protection (5.3%). This translates to a density benefit of 2.2 orangutans per 25 km² for every annual spending of US\$10,000 for each activity of outreach and habitat protection. In Sumatra, patrolling had the highest benefit-per-dollar (average improvement of 16% in occurrence probability per 5×5 km² grid-cell per US\$10,000 annual investment relative to the counterfactual). This translates to a density benefit of 2.3 orangutans per 25 km² for every annual spending of US\$10,000.

Discussion

Implications for orangutan conservation policies in different regions

Kalimantan

In Kalimantan, habitat protection produced the best outcome in reducing the decline in orangutan probability of occurrence (Figure 5b). Large-scale forest loss and the expansion of industrial agriculture, especially in unprotected lands (in non-state-forest zones and forest areas designated for land clearing and conversion to agro-industries) occurred at rapid rates, especially between 2005 and 2015¹⁵. These lowland areas typically co-occur with orangutan populations, and without forest protection extensive areas of

orangutan habitats and subsequently large populations of orangutans would have been lost. The average investment per km² for habitat protection in Kalimantan was generally lower than in Sumatra and Sabah (\$252 per km², versus \$734 and \$664 per km² for Sumatra and Sabah respectively) (Figure 4b), reflecting Kalimantan's earlier stage of development compared to the other two regions ¹⁶. Consequently, habitat protection by government, companies or rural communities was considered to provide an excellent return-on-investment in reducing the decline in orangutan occurrence (Figure 6b).

Annual spending on translocation and reintroduction in Kalimantan had increased fourfold since 2000 (from \$0.7 million in 2000 to \$2.8 million in 2019) (Figure S5), and this reflects the growing application of this conservation tool in response to increasing land pressure. Rapid large-scale deforestation over the past 20 years has led to escalated negative interactions between humans and wild orangutans ^{4,5,10}. Rescue and translocation of orangutans to conservation areas or protected forests have provided readily implementable actions to remove animals from immediate danger arising from such negative interactions. Removing orangutans and translocating them to large forest blocks deemed more suitable for their survival may seem straightforward and is often presented as an efficient conservation tool, particularly when alternative conservation activities may require planning and extensive negotiation with multi-sectoral and multi-level stakeholders ¹⁷. However, the relative success of this conservation approach is still not known and might be relatively low and there is a potential negative impact of these exercises on the viability of metapopulations ¹⁷. Furthermore, translocation and reintroduction can be costly and are associated with high mortality rates ¹⁸. In Kalimantan, translocations were the most expensive conservation activities in terms of operational cost per km², and the cost greatly exceeds those in other regions (\$427 per km², versus \$41 and \$121 per km² for Sabah and Sumatra) (Figure 4b).

The number of orangutans residing outside of protected areas is substantial in Kalimantan ^{4,5}. Hence, continuing land clearing in this region is anticipated to lead to frequent negative interactions between orangutans and people, and potentially higher prevalence of orangutan removal. An ongoing and increasing focus on translocation and reintroduction programs in Kalimantan could potentially undermine the allocation of funding to other activities with substantially higher and lasting benefits such as habitat protection, patrolling, and outreach programs. There is a need to seek solutions that would enable

orangutans and people to co-exist, such as better land use planning through creation of buffer zones separating orangutan habitats and rural settlements and improved partnership between conservation actors and rural communities in building relationships of reciprocity, acknowledgment, and care ¹⁹.

The expenditure cost per square kilometre for habitat protection in Kalimantan was generally lower than in other regions (Figure 4b), suggesting that it is relatively inexpensive to effectively reduce orangutan declining rates through this action. Habitat protection is therefore a worthy investment to pursue to allow orangutans to remain in their native habitats in this region. Further, given that the current conservation expenditure per square kilometre of orangutan habitat in Kalimantan is substantially lower than in other regions (Figure 2c), increasing the amount of investment for habitat protection here could potentially reduce the orangutan declining rates significantly.

The costs associated with patrolling activities in Kalimantan were \$155 per km² and significantly lower than in other regions (\$1,303 and \$302 per km² for Sabah and Sumatra respectively), whereas outreach programs were \$93 per km² and also lower than in other regions (\$491 and \$204 per km² for Sabah and Sumatra) (Figure 4b). This is likely because human population density, remuneration rates and market influence in Kalimantan are generally lower compared to other regions ¹⁶. Larger investments can therefore potentially be allocated to these activities to monitor, prevent negative human-wildlife interactions, and assist rural communities living within close proximity to forests inhabited by orangutans ¹⁴. Local communities are also likely to benefit from maintaining forest cover, as forests can support and sustain the flow of ecosystem services and provide benefits to broader community wellbeing (e.g., by preventing soil erosion and floods, and regulating air quality) ²⁰⁻²².

Sabah

In Sabah, patrolling produced the best outcome in reducing the decline in orangutan occurrence probability, followed by habitat protection (Figure 5b). During the study period, the Sabah government increased the size of protected areas from 12% to nearly 30% of the state land area ^{23,24}, and, by 2020, more than 70% of orangutans in Sabah were found inside protected areas ^{17,23}. This is quite different from the situation in Indonesia where most terrestrial protected areas were established before 2005 (currently

covering 23% of the total land area for Kalimantan and Sumatra), and the expansion of forest protection since 2005 was mainly through the establishment of community-based land tenure and acquisition of private land by conservation NGOs. Consequently, a high level of investment specifically from the Sabah government has been allocated to resource-intensive patrolling activities for these protected areas, but lower investment had been allocated to habitat protection since all these new areas were gazetted by the government without incurring any high significant direct cost or land purchase for their creation. Significantly higher baseline remuneration rates in Malaysia compared to Indonesia^{25,26} have also likely contributed to the high cost associated with patrolling activities.

Public outreach programs, community engagement and capacity building also provided benefits to protecting orangutan populations in Sabah (Figure 5b), and these programs were mainly carried out by various state agencies and their NGO partners. Despite higher operational cost per square kilometre for public outreach in Sabah than in Kalimantan and Sumatra (\$491 per km², versus \$93 and \$204 per km² for Kalimantan and Sumatra) (Figure 4b), the activity provided the best return-on-investment in terms of orangutan occurrence benefits (Figure 6b). Unlike in Kalimantan and Sumatra, there has been limited change in land cover in Sabah over the past 20 years as deforestation had mostly occurred before 2000¹⁵. Consequently, only a low number of orangutan individuals were displaced and required rehabilitation or translocation between 2000 and 2019, and this explains why the expenditures for rehabilitation and reintroduction programs were small (Figure 4).

Sumatra

In Sumatra, habitat protection produced the best outcome in reducing the decline in the orangutan's probability of occurrence, followed by patrolling activities (Figure 5b). However, the cost of habitat protection was expensive compared to the cost of other activities in the region, and compared to habitat protection in other orangutan regions in Indonesia (\$735 per km², versus \$252 per km² for Kalimantan) (Figure 4b). This is likely attributed to the higher opportunity cost of land for conversion to agriculture, and the cost associated with establishing and managing land in this relatively developed region¹⁶. During the study period, several land acquisitions and their protection occurred across the orangutan range in Sumatra (e.g., within the Leuser Ecosystem). Such initiatives, consequently, incurred significant direct

costs on land purchase and management establishment. Despite providing the highest benefit on orangutan occurrence (Figure 5b), due to the high land-related cost (Figure 4b) the protection strategy was considered less efficient in terms of monetary value (Figure 6b). On the other hand, the costs of patrolling were moderate (\$302 per km²), which is higher than in Kalimantan (\$155 per km²) but substantially lower than in Sabah (\$1,303 per km²) (Figure 4b). This could be partly due to the lower baseline remuneration rates in Indonesia compared to Malaysia, despite baseline prices of goods in both countries being relatively similar^{25,26}. Due to the moderate costs for patrolling, this activity provided the best return-on-investment in terms of orangutan occurrence benefit in Sumatra (Figure 6b).

Rescue and rehabilitation activities provided only a small benefit for maintaining the probability of occurrence of orangutans in their range (i.e., they provide limited deterrence to poaching and trafficking), and this is similar to the presence of reintroduction sites and outreach activities in the island (Figure 5b). Similar to the situation in Sabah, the investment in rehabilitation activities in Sumatra was minor (Figure 4), hence the return-on-investment for probability of occurrence has limited applicability.

Caveats and limitations

There are four key limitations in our analysis. The first pertains to the accuracy of our investment dataset. While we attempted to comprehensively collect information on all investment, it is likely that we missed a few. Additionally, in some instances, detailed information on the amount of investment for different activities for a particular organization was not available. To overcome this issue, we estimated activity expenditure amounts based on the activities described in the organization's reports or website and the costs of those activities undertaken by similar-sized organizations operating in the same region for which we had specific data. The second limitation is associated with the modelling approach and the implications on the estimation of conservation benefits. We assumed that the effect of a conservation activity on orangutan presence can be adequately captured in the model mainly through variable distance to the location of that conservation program as a proxy (see Methods). As such, in a grid-cell where multiple activities are operating simultaneously with different levels of importance (e.g., patrolling is carried out with higher efforts than public outreach programs), the model assumes equal importance of all actions. As research programs usually co-occur simultaneously with other conservation activities, the impact of research is

difficult to estimate accurately through our modelling approach. This was the reason why we excluded research from the cost-benefit analysis. The third limitation relates to the methodology for constructing the counterfactual scenarios. We applied the most sensible, relevant and practical approach for defining the counterfactuals. In reality, these counterfactual scenarios are much more complicated and influenced by multiple biophysical and socioeconomic factors ²⁷. The fourth limitation pertains to province-level differences in threats and government policies in Indonesia. Our cost-benefit analyses were aggregated to provide general and broad island-based inference to inform national policies. Province-level analysis would likely generate more nuanced outcomes from the modelling output to guide local policy at the sub-island level. We have tried to adequately address these limitations wherever possible and are convinced that despite these caveats the results of the analysis reflect appropriately the situation on the ground.

Conclusions and recommendations

Judicious planning for conservation under a constrained budget requires an understanding of the dynamics of conservation investments and activities and how they relate to species trends across their spatial range. Such an analysis is however rarely conducted, as it requires comprehensive spatiotemporally explicit data on the species, the natural environment and threats, conservation activities, investments in these activities, and an estimation of the counterfactual situation without the investment. Using orangutans as a case study, our analysis estimated that habitat protection, patrolling and public outreach provided large benefits in slowing down the decline in orangutan numbers. However, given variability in threats and development circumstances and stages in different regions where orangutans occur, the most cost-effective conservation activity was different across regions. Our findings highlight the importance of accounting for regional differences in land pressure and socioeconomic elements to guide the focus of investment in different areas and contexts to achieve the desired conservation goals.

We recommend the application of our findings in planning for future funding and policy strategies for orangutan conservation to ensure optimal use of limited resources and apply the analytical framework to the conservation of other wildlife. It would be highly beneficial for orangutans and other species if data on their distribution and densities and detailed information on conservation programs, (i.e., where are they conducted and when, what kind of activities specifically involved, and how frequent these activities are

conducted) could be transparently and centrally coordinated, made publicly available, and regularly updated by participating organizations working in species conservation. Such transparency on spending could help facilitate open discussions about improving the existing strategies.

Acknowledgements

We thank the United States Fish and Wildlife Service; the Arcus Foundation; Orangutan Foundation UK; Natural Sciences and Engineering Research Council of Canada (NSERC); Nacey Maggioncalda Foundation; Leakey Foundation; University of Wisconsin Oshkosh; Disney Conservation Fund; Direktorat Perguruan Tinggi Republik Indonesia; the Sabah Biodiversity Council for research approval (ref: JKM/MBS.1000-2/2 JLD.6 (79)); the Department of Aviation Malaysia (ref: UMS/IBTP7.2/800); Yayasan Sabah Sdn. Bhd; Charles Garcia and Ronnie Bibi; the Sabah Forestry Department; UNDP-GEF for funding; Darwin Initiative for the Survival of Species (Grant no. 09/016, DEFRA, UK); Nacey Maggioncalda Foundation; and University of Wisconsin Oshkosh.

Author contributions

Conceptualization, E.Me., T.S., J.S., M.V., M.A., S.A.W. and K.A.W.; Methodology, T.S., E.Me., J.S., M.V., M.A., S.A.W., K.A.W., H.P. and D.J.I.S.; Software, T.S. and M.V.; Formal Analysis, T.S., E.Me., J.S., M.V., M.A., and S.A.W.; Investigation, E.Me., T.S., J.S., M.V., M.A., S.A.W., E.Me., D.J.I.S., A.M.A., T.S.A., G.L.B., E.J.B., D.F.R.P.B., R.A.D., A.E., G.F., B.G., M.H., T.P.I., R.L.J., T.K., C.D.K., A.L., D.L., M.M., A.J.M., J.G.A.M., L.M., A.M., S.M., C.M., N., D.P-F., D.P., R.R., G.M.R., A.R., J.S., E.S., M.S., D.S., S.S., M.J.S., I.S., A.T., R.Z. and A.Y.; Data Curation, E.Me., T.S., J.S., M.V., M.A., S.A.W.; Writing – Original Draft, E.Me., T.S., J.S., M.V., M.A., S.A.W. and K.A.W.; Supervision, J.S., M.A., E.Me; Project Administration, J.S., Funding Acquisition, J.S., M.A., E.Me., S.A.W., and K.A.W.

Declaration of interests

The authors declare no competing interests.

Main-text figure titles and legends

Figure 1. Islands covering the orangutan range.

Sumatra, Indonesia (470,000 km²) and Borneo (including Kalimantan, Indonesia and Sabah and Sarawak, Malaysia) (740,000 km²). See also Figure S4.

Figure 2. Changes in nominal and real investments into orangutan conservation over time and by region.

(A) Total investment (nominal and real value, in US\$) spent annually on orangutan-related conservation activities across Kalimantan, Sabah and Sumatra. (B) The annual total real expenditure of conservation activities, and (C) per km² of orangutan habitat, broken down by region. Conservation activities assessed include the six core activities in which the impacts on orangutan survival may be captured over a short time period (five years): habitat protection, habitat restoration, patrolling and law enforcement, rescue and rehabilitation, translocation and reintroduction, and public outreach and capacity building, and research-related activities considered influencing conservation and land use management decision in the long term.

Figure 3. The change in the distribution of investment to orangutan conservation in Borneo and Sumatra, aggregated to sub-district level.

Values inside the parenthesis represent the annual total real expenditure for a given period and region. In the first period (2000-2004), investments in Borneo were focused in Sabah and spread across the orangutan range in West, Central and East Kalimantan. Investments in later periods gradually became clustered more around orangutan sanctuaries near the Gunung Palung, Tanjung Puting, Sebangau, and Kutai National Parks and the interior part of Borneo. In Sumatra, the main increase in investment was in the Jantho Nature Reserve at the northern part of the island and Batang Toru. Relates to Figure S5.

416

417 **Figure 4. Expenditure allocation to different strategies.**

418 (A) Proportion of total expenditure allocated to different conservation activities, and (B) mean annual real
419 expenditure for different activities (US\$ per km²) broken down by region. The costs of conservation
420 activities assessed include the six core activities considered affecting the orangutan survival in the short
421 term (five years): habitat acquisition and protection (PROTECT), habitat restoration (RESTORE),
422 patrolling and law enforcement (PATROL), rescue and rehabilitation (REHAB), translocation and
423 reintroduction (REINTRO), and public outreach and capacity building (OUTREACH), and research-
424 related activities considered influencing orangutan persistence in the long term (RESEARCH). See also
425 Figure S5.

426

427 **Figure 5. The benefit of six orangutan conservation activity within the wild orangutan contemporary**
428 **range.**

429 (A) estimated by comparing the orangutan probability of occurrence (given existing conservation actions)
430 with the counterfactual in the absence of conservation activity, (a) averaged across the three regions, and
431 (B) individually by region. Conservation activities evaluated include the six core activities: habitat
432 protection (PROTECT), habitat restoration (RESTORE), patrolling and law enforcement (PATROL),
433 rescue and rehabilitation (REHAB), translocation and reintroduction (REINTRO), and public outreach and
434 capacity building (OUTREACH). Research-related activities (RESEARCH) was excluded from the
435 benefit analysis as it is considered to primarily influence conservation actions and land use management
436 decisions in the long term. See also Figure S4.

437

438 **Figure 6. Return-on-investment of six orangutan related conservation activities.**

439 Defined as the percentage improvement in orangutan probability of occurrence per 5x5 km² per US\$10,000
440 investment. (A) overall across the three regions, and (B) broken down by region. Conservation activities
441 assessed include the six core activities: habitat protection (PROTECT), habitat restoration (RESTORE),
442 patrolling and law enforcement (PATROL), rescue and rehabilitation (REHAB), translocation and
443 reintroduction (REINTRO), and awareness raising, capacity building and policy (OUTREACH). Research-
444 related activities (RESARCH) was excluded from the return-on-investment analysis as it is considered as
445 primarily influencing conservation actions and land use management decisions in the long term.

STAR Methods

Resource availability

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Truly Santika (T.Santika@greenwich.ac.uk).

Materials availability

This study did not generate new unique reagents.

Experimental model and subject details

We collected data on orangutan conservation investments across Borneo and Sumatra for the period 2000–2019, based on the most recent yearly budget allocations available, comprising a total of 259 investments. We identified initial lists of organizations that were carrying out orangutan conservation activities. An organization was considered conducting orangutan conservation activities if it met two criteria:

- 1) the goals or conservation activity descriptions specifically mentioned orangutans, or in the case of habitat conservation activities orangutans were specifically mentioned in relation to the affected habitat; and
- 2) the orangutan-related conservation activities were conducted on the ground in the orangutan range regions (Borneo and Sumatra) regardless of where the organization was headquartered.

For every investment, we recorded the entity or organization managing the conservation activity, the sector of the entity (e.g., government agency, non-government organization (NGO), and rescue centres), the location where the activity had taken place, the allocation of funds spent on each category of conservation activities during the latest available financial year (see below), the years between 2000 and 2019 when the activities were undertaken, and the investment amount.

Other data used are detailed in the Key Resources Table.

Method details

Our study framework consists of four steps of analyses: (1) collating data on conservation investments; (2) modelling the change in the distribution of the species under study; (3) estimating the benefit of conservation activities on that species through changes in the species occurrence; and (4) estimating the return-on-investment.

Our study area covers the orangutan range in the island of Sumatra, Indonesia (470,000 km²) and Borneo (including Kalimantan, Indonesia and Sabah, Malaysia) (740,000 km²) (Figure 1). We excluded the Malaysian state of Sarawak, as we have insufficient data on orangutan surveys and conservation investment in this region. The orangutan range in Sarawak is small compared to the overall orangutan range and leaving out Sarawak should not affect our overall findings. For the spatial unit of analysis, we used a grid-cell with a resolution of 5×5 km². This resolution corresponds to the average home range of adult male orangutans, which overlaps with the home range of several females ²⁸. As the temporal unit of analysis, we used four time periods: 2000-2004, 2005-2009, 2010-2014, and 2015-2019.

Collecting data on conservation investments

We collected investment data through direct communications with identified organizations, and via desktop research and review of publicly available data on each organization's expenditure reports (i.e., grant and project databases, corporate sustainability reports, annual reports, budgets and financial reports, tax filings of donors and implementing organizations and charity commission reports, and organization websites) (see Tables S1 and S2 for the source of information on investment and the list of organizations or entities). To avoid double counting investments from both donors and implementers, we only used data on investments made by organizations implementing orangutan conservation activities on the ground in orangutan habitat.

Where an organization's investment amounts by activity were not specified (data were only available on the overall amounts), we looked for data from any project grants related to orangutan conservation the organization received where amounts spent on specific activities were detailed. Where no detailed data was available for a given organization, we estimated activity expenditures amounts based on the activities

described in the organization's reports or website, and the costs of those activities undertaken by similar-sized organizations operating in the same region for which we did have specific data. We tested these estimations for accuracy by requesting selected organizations to check our figures for their budgets. For government-funded habitat protection activities, we also included community-based forest management, especially the *Hutan Desa* (Village Forest) scheme in Indonesia. We only included *Hutan Desa* areas where the boundaries overlap with the orangutan range. We used an estimated cost of US\$50 per ha for establishing *Hutan Desa*²⁹. For oil palm concessions certified under the Roundtable on Sustainable Palm Oil and timber concessions certified under the Forest Stewardship Council where no sustainability investment was specified, we estimated that US\$10 per ha (RSPO) or US\$1 per ha (FSC) was spent on HCV areas. These averages were based on data from several companies for which we had more detailed information on investment per unit area. The expenditure data we collected from various organization reports and databases were mostly in US\$ (US Dollar). The amounts of spending in a given year originally provided in national currencies (Indonesian Rupiah and Malaysian Ringgit) were converted to US\$ using the currency conversion rate applicable to that year.

We categorized organizations into six sectors: (1) government, including agencies, national parks, and government-funded community-based forest management; (2) bilateral or multilateral bodies; (3) non-governmental organizations (NGOs); (4) rescue centres, including sanctuaries for care of orphaned or seized wildlife, (5) commercial corporations including industrial agriculture, timber and pulp, logging, and mining; and (6) research centres and universities. For commercial corporations, oil palm plantation companies certified by the Roundtable for Sustainable Palm Oil (RSPO) that spent funds to maintain High Conservation Value lands which were known to have orangutans (based on the overlap with the species' ranges) were included even if the company reports did not specifically mention orangutan conservation. We did the same for timber plantations and logging companies certified by the Forestry Stewardship Council (FSC). This is because both RSPO and FSC require the conservation values (including orangutans) in the concession to be maintained, and independent audits are carried out to verify this^{30,31}. We assumed that uncertified plantations, logging, or mining concessions did not invest in orangutan conservation unless our review of orangutan investment information identified them specifically as doing so. For research, funding for local studies of orangutans by researchers (local and foreign) was counted if: (1) the research

was part of the work of an in-situ research centre focused on orangutans or including orangutan studies, and the studies met both criteria mentioned above; or (2) the research project came up in search results for orangutan conservation investments and met both our criteria. Investments in orangutan habitat range by government agencies with direct management authority for orangutans or any orangutan habitat areas were included regardless of orangutan mentions.

For missing annual data on investment, we estimated the amount of spending by fitting an Ordinary Least Square (OLS) regression model to the available data covering different years. For an entity with limited investment data, we estimated the overall investment envelope based on the trends captured in similar-sized organizations. For NGOs and rescue centres, we identified a consistent pattern of a 2-3% increase in annual expenditure for orangutan conservation between 2000 and 2019 across Indonesia and Malaysia. Similarly, we identified a 4-5% increase in government's annual expenditure for orangutan conservation over the same period in Malaysia and wildlife conservation activities in general for Indonesia. For that reason, we applied 2.5% and 4.5% annual increases for missing NGO data and missing government data, respectively.

Allocating investment data to activities

Expenditure data by individual activities were not consistently available from all orangutan conservation entities, hence we grouped similar activity types into the six broad categories described below. For each investment unit, we first recorded the entity, entity sector, the location where the entity was operating, and funds spent during the latest available financial year on six categories of conservation activities based on the Conservation Measures Partnership Action Classifications³². Six categories of activities related to orangutan conservation were identified across the three regions. The classification of activities were informed by the Conservation Measures Partnership³² and include: (1) habitat protection and acquisition (PROTECT); (2) habitat restoration (RESTORE); (3) patrolling and law enforcement (PATROL); (4) rescue and rehabilitation (REHAB); (5) translocation and reintroduction (REINTRO); and (6) public outreach and awareness raising, capacity building and policy (OUTREACH) (Figures S1 and S2). Besides these six core activities, we also estimated investment in research activities that may influence

conservation and land use management decisions (RESEARCH) (Figure S3). Details about the activity categories are as follows:

- 1) Habitat protection and acquisition (PROTECT), includes management and maintenance of the land, such as firefighting, invasive plant or animal control, fencing or other infrastructure related to protection, avoided deforestation payments or costs, habitat purchase, community land reserves or forestry including payment to communities to establish protection;
- 2) Habitat restoration (RESTORE), includes replanting, growing nursery stock, maintenance of restored forest by watering, and other activities needed to establish and maintain restored habitat;
- 3) Patrolling and law enforcement (PATROL), includes rangers and wardens and their associated expenses, infrastructure like guard posts, patrol equipment, prosecution, and incarceration costs;
- 4) Rescue and rehabilitation (REHAB), includes activities related to intake, captive care and rehabilitation of orangutans;
- 5) Orangutan reintroduction and translocation (REINTRO), includes orangutan releases, post-release monitoring and research to identify release sites or release outcomes. Orangutan releases include: (a) the release of rehabilitated ex-captive orangutans to reinforce existing wild populations; (b) reintroduction of populations within historic range but outside the current distribution; and (c) removal and subsequent release of wild orangutans considered an immediate or potential threat to humans and human activities, or where the orangutans are themselves threatened by humans and human activities; and
- 6) Public outreach, awareness raising, capacity building and policy (OUTREACH), includes community outreach, training and capacity building for environmentally friendly livelihoods and human-orangutan conflict mitigation, policy development or advocacy on orangutan conservation related issues.

An additional expenditure category of administrative and overhead costs (costs for operation of the entity rather than the implementation of activities) was excluded from our model. Although the cost of operating

the organizations, businesses and agencies is vital to the ability to deliver the orangutan conservation activities, and represents millions more dollars spent annually, these expenditures did not meet our criteria of conservation activities implemented within orangutan range.

Orangutan conservation Theory of Change (ToC) pathways

The Theory of Change (ToC) pathways for each orangutan conservation activity (Figures S1, S2 and S3) represent the chain of outcomes resulting from the conservation activities within the short term (five years after the activity is initiated) and long term (more than five years after initiation) that can lead to reduced threats and positive impacts on species population trends. We considered the short term, five-year time interval in the ToC to conform to the data analysis and modelling approach we used. Under this ToC framework, it is assumed that PROTECT actions establish land regulation, management and enforcement to prevent habitat degradation and poaching. RESTORE actions facilitate forest regrowth, either through active restoration (e.g., reforestation and hydrological rehabilitation) or passive restoration (natural regeneration). The presence of PATROL activities helps reduce wildlife and forest crimes, and law enforcement actions can further establish this deterrence. REHAB includes the transfer of animals seized by authorities, a preliminary step in a legal process that, when it culminates in sanctions, can deter crime. Additionally, REHAB actions provide opportunities for releasable animals to become part of a successful release program. REINTRO actions facilitate orangutans released into natural habitats where they can improve the viability of existing wild populations or establish new viable populations. REINTRO actions can also pose real disease, genetic and behavioural risks to wild orangutan populations, and thus have the potential to have both positive and negative impacts on the species. OUTREACH actions assist communities in mitigating human-orangutan conflicts and supporting behavioural changes to facilitate coexistence between orang-utan and people and support conservation of orangutans and their habitats. Unlike these six core conservation activities whereby the benefits on orangutan survival are likely to be realized over the short term (within five years period), RESEARCH activities may take longer time to benefit orangutans. Most research consists of several stages of activities (e.g., field survey and data collection, data analysis, and consultation with different stakeholders) that may take several years to produce findings to inform or provide recommendations for conservation actions and policies. These

policy recommendations subsequently may take several more years to be implemented and therefore begin to benefit the species. Nonetheless, research sites whereby researcher presence is maintained over the long term are recognized to have a deterrent effect on poaching and forest crimes³³.

Orangutan survey data

We used an existing database of orangutan survey data from 2000 to 2015^{2-5,17,34,35} and new survey data from 2015 to 2019, from both Borneo and Sumatra. These data consisted of: (a) orangutan nest encounters obtained from transects surveys, both on the ground and from aerial surveys (occupied aircraft and drones); (b) orangutan or nest encounters obtained from reconnaissance or opportunistic surveys; and (c) sightings of orangutans reported by village residents through interviews. To reduce potential false detection of orangutans in the interview data, we selected only villages where more than 30% of respondents reported orangutan sightings as an indicator of orangutan presence. For each time period, any 5×5 km² grid-cell with orangutan sightings or nest encounters was assigned “presence”, whereas grid-cells with one survey or more without any sightings of orangutans or nests was assigned “absence”. Absence records in a grid-cell for a given time period can therefore represent real absence (the species never occurred in that grid-cell) or loss (the species used to be present in that grid-cell, but not anymore). Grid-cells without any survey were excluded in the model building.

Quantification and statistical analysis

Inflation-adjusted value of investment

The investment data represent the nominal value of investment. To obtain the real value of investment to facilitate intra-country comparison and discern the actual purchasing power of organizations in implementing activities on the ground across different regions, we adjusted the nominal value with inflation rates³⁶. Inflation rates have changed dramatically in Indonesia and Malaysia between 2000 and 2019 (<https://data.worldbank.org/indicator/NY.GDP.DEFL.KD.ZG>). The consumer price indices (CPI) in both countries are similar and therefore were not employed in the adjustment. The real value of investment in time period 2000-2004 ($t=1$), 2005-2009 ($t=2$), and 2010-2014 ($t=3$) can be expressed in reference to the present period 2015-2019 ($t=4$), i.e.

$$\hat{C}_t = C_t \times (r_1 + 1)^{5 \times b_1} \times (r_2 + 1)^{5 \times b_2} \times (r_3 + 1)^{5 \times b_3}$$

with $(b_1, b_2, b_3) = (1, 1, 1)$ if $t=1$,

$(b_1, b_2, b_3) = (0, 1, 1)$ if $t=2$, or

$(b_1, b_2, b_3) = (0, 0, 1)$ if $t=3$.

where \hat{C}_t is the real value of investment at time period t relative to the present period; C_t is the nominal value of investment at time period t ; and r_1 , r_2 and r_3 is the average inflation rates for time period $t=1$, $t=2$, and $t=3$, respectively.

We aggregated the yearly investment data into four time periods to conform to the baseline time interval used in the orangutan occurrence change analysis: 2000-2004, 2005-2009, 2010-2014, and 2015-2019. We also calculated the estimated investment in each 5×5 km² grid-cell for each of the six activities plus investments into orangutan-related research.

Modelling the change in species distributions

We used the Generalized Boosted Regression Modelling (GBM) approach³⁷ to fit the orangutan presence-absence data for each of the four time periods for each orangutan region (i.e. Kalimantan, Sabah, and Sumatra) using 15 environmental predictors (Table S3). These regional divisions were chosen to account for the broad threat and socioeconomic patterns and government policies at the national and island levels. The environmental predictors included static variables over the timeframe of interest, such as elevation, long-term mean monthly rainfall during the dry and wet months, distance to nearest city, and percentage of peatland, and dynamic variables (with changing spatial configurations over the different time periods t), including forest cover ($FORST_t$), percentage of degraded peatland (<30% forest cover) ($DEGPT_t$), distance to nearest industrial oil palm plantation, and distance to conservation activities that are considered to be delivering benefits to orangutans. These conservation activities included forest protection through the establishment of protected areas (including national parks, nature reserves, watershed protection forest, and community-based forest management) ($PRTCA_t$), patrolling activities ($PTROL_t$), rehabilitation centres ($RHCTR_t$), orangutan translocation and reintroduction sites ($RINTR_t$), and orangutan-related public

outreach and awareness raising (*COMRC_i*). To control for spatiotemporal effects of survey protocols on orangutan presence reports, we included survey effort (i.e., the number of surveys on orangutans conducted in each grid-cell) and distance to orangutan research centres or activities as predictor variables. All predictor variables were weakly correlated.

For each regional-based GBM model, we estimated the model parameters (Figure S6) and the change in the probability of occurrence of orangutans through the four time periods in each region. The baseline probabilities of occurrence differed between regions. To standardize the change in occurrence across the different regions, and to provide a practical representation of the population change through time to inform policy, we translated the probability of occurrence data to density estimates. This was done by assessing the correlation between the predicted orangutan probability of occurrence (generated from the GBM) and the density rates calculated directly from the orangutan transect dataset over grid-cells where transect surveys were conducted (Figure S4).

Estimating the benefit of conservation activities and the return-on-investment

The counterfactual scenario, reflecting the absence of conservation activity between 2000 and 2019, was calculated by estimating how each activity modifies the predictor variables in the GBM models. The association between the outcome potentially generated from each activity and the predictor variables was informed by the orangutan conservation Theory of Change (ToC) pathways (Supplementary Data; Figures S1 and S2). The habitat protection strategy (PROTECT) is assumed to affect forest loss and ecosystem protection more broadly²⁰. Our analysis suggested that areas assigned to protected areas were able to halve deforestation rates (compared to the rates within 50 km of the protected area boundaries) in Borneo and reduce deforestation rates by a quarter in Sumatra (Figure S7A), and this is likely because pressure to convert forest to other land uses was stronger in Sumatra than in Borneo overall^{16,38}. Hence, the counterfactual scenario in the absence of PROTECT assumes that: (a) the counterfactual forest loss rates inside protected areas were roughly twice or four times the actual rates for Borneo and Sumatra respectively (i.e. $FORST_{1,counterfactual} = FORST_0 - (r \times FLOSS_1)$, and $FORST_{t,counterfactual} = FORST_{t-1,counterfactual} - (r \times FLOSS_t)$ for $t > 1$, where $r=2$ for Borneo and $r=4$ for Sumatra), (b) the counterfactual percentage of degraded peatland (<30% forest cover) inside protected areas ($DEGPT_{t,counterfactual}$) is higher than the actual

679 ($DEGPT_t$); and (c) the counterfactual distance to forest protection was the actual distance multiplied by 100
680 (i.e. $PRTCA_{t,counterfactual} = PRTCA_t \times 100$), thus forest protection having negligible effect.

681 The habitat restoration strategy (RESTORE) is assumed to affect forest gain. Our analysis suggested that
682 areas assigned to habitat restoration in Borneo and Sumatra were able to increase forest cover twice the
683 rate outside habitat restoration areas (Figure S7B). Hence, the counterfactual scenario in the absence of
684 RESTORE assumes that the counterfactual forest gain inside restoration areas was half the actual forest
685 gain (i.e. $FORST_{1,counterfactual} = FORST_0 + (0.5 \times FGAIN_1)$, and $FORST_{t,counterfactual} = FORST_{t-1,counterfactual} +$
686 $(0.5 \times FGAIN_t)$ for $t > 1$).

687 For conservation activities such as patrolling and law enforcement (PATROL), rescue and rehabilitation
688 (REHAB), translocation and reintroduction (REINTRO), and outreach and advocacy (OUTREACH), the
689 counterfactual scenario in the absence of the activity assumes that the counterfactual distance to the
690 activity was the actual distance multiplied by 100 (i.e. $PTROL_{t,counterfactual} = PTROL_t \times 100$ for PATROL,
691 $RHCTR_{t,counterfactual} = RHCTR_t \times 100$ for REHAB, $RINTR_{t,counterfactual} = RINTR_t \times 100$ for REINTRO, and
692 $COMRC_{t,counterfactual} = COMRC_t \times 100$ for OUTREACH). Our analysis suggested that deforestation rates in
693 areas with PATROL, REINTRO, or OUTREACH activities were similar to the rates in areas without such
694 activities. Therefore, we assumed that the counterfactual forest cover is the same as the actual.

695 The benefit of each conservation activity in each 5×5 km² grid-cell was estimated as the percent
696 improvement in the orangutan probability of occurrence compared to the counterfactual scenario. Specific
697 for the translocation and reintroduction strategy (REINTRO), we further multiplied the benefit by 50%.
698 This is considering that post-release mortality rates of orangutan individuals in new translocation areas can
699 range widely between 20% and 80%^{18,39,40}, thus the median value of 50% was chosen. In calculating the
700 benefit, we focussed only on activities that had occurred within the contemporary ranges of wild
701 orangutans, therefore excluded reintroduction sites outside the orangutan range such as the Jantho Nature
702 Reserve and Bukit Tigapuluh National Park in Sumatra.

703 Return-on-investment from orangutan conservation activity in each 5×5 km² grid-cell was estimated as the
704 benefit of conservation activity in improving orangutan probability of occurrence compared to the

counterfactual scenario divided by the cost of activity in that grid-cell. The conservation activities with the largest return-on-investment will deliver the largest improvements in orangutan occurrence per dollar.

Data and code availability

- The raw investment data and orangutan survey data reported in this study cannot be deposited in a public repository because of confidentiality issues. To request access, ask the lead contact for contact information for the entities listed in Tables S1 and S2. In addition, processed datasets derived from these data have been deposited at the APES database (<http://apesportal.eva.mpg.de/>) and will be publicly available as of the date of publication. Accession numbers or DOIs are listed in the Key Resources Table.
- This paper analyzes existing, publicly available data. The accession numbers for the datasets are listed in the Key Resources Table.
- All non-confidential data reported in this paper will be shared by the lead contact upon request.
- All original code is available in this paper's supplemental information.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

R code

All original code has been deposited at DOI: 10.5281/zenodo.6080322 and is publicly available as of the date of publication. DOIs are listed in the key resources table.

References

1. Cook, C.N., Pullin, A.S., Sutherland, W.J., Stewart, G.B., and Carrasco, L.R. (2017). Considering cost alongside the effectiveness of management in evidence-based conservation: A systematic reporting protocol. *Biological Conservation* 209, 508-516. 10.1016/j.biocon.2017.03.022.
2. Wich, S.A., Singleton, I., Nowak, M.G., Utami Atmoko, S.S., Nisam, G., Arif, S.M., Putra, R.H., Ardi, R., Fredriksson, G., Usher, G., et al. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). *Science Advances* 2, e1500789. 10.1126/sciadv.1500789
3. Utami-Atmoko, S., Traylor-Holzer, K., Rifqi, M.A., Siregar, P.G., Achmad, B., Priadjati, A., Husson, S., Wich, S., Hadisiswoyo, P., Saputra, F., et al. (2019). Orangutan Population and Habitat Viability Assessment: Final Report (unpublished). IUCN/SSC Conservation Breeding Specialist Group.
4. Voigt, M., Wich, S.A., Ancrenaz, M., Meijaard, E., Abram, N., Banes, G.L., Campbell-Smith, G., d'Arcy, L.J., Delgado, R.A., Erman, A., et al. (2018). Global Demand for Natural Resources Eliminated more than 100,000 Bornean Orangutans. *Current Biology* 28, 761-769.e765. 10.1016/j.cub.2018.01.053.
5. Santika, T., Ancrenaz, M., Wilson, K.A., Spehar, S., Abram, N., Banes, G.L., Campbell-Smith, G., Curran, L., d'Arcy, L., Delgado, R.A., et al. (2017). First integrative trend analysis for a great ape species in Borneo. *Sc. Rep.* 7, 4839. 10.1038/s41598-017-04435-9.
6. Ancrenaz, M., Gumal, M., Marshall, A.J., Meijaard, E., Wich, S.A., and Husson, S. (2016). *Pongo pygmaeus*. The IUCN Red List of Threatened Species 2016, e.T17975A17966347.
7. Nowak, M.G., Rianti, P., Wich, S.A., Meijaard, E., and Fredriksson, G. (2017). *Pongo tapanuliensis*. IUCN Red List Threat. Sp., e.T120588639A120588662. 10.1111/csp2.33.
8. Singleton, I., Wich, S.A., Nowak, M., Usher, G., and Utami-Atmoko, S.S. (2017). *Pongo abelii*. IUCN Red List Threat. Sp., e.T121097935A115575085.
9. Davis, J.T., Mengersen, K., Abram, N., Ancrenaz, M., Wells, J., and Meijaard, E. (2013). It's not just conflict that motivates killing of orangutans. *PLoS ONE* 8, e75373. 10.1371/journal.pone.0075373.
10. Abram, N.K., Meijaard, E., Wells, J.A., Ancrenaz, M., Pellier, A.-S., Runting, R.K., Gaveau, D., Wich, S., Nardiyono, Tjiu, A., et al. (2015). Mapping perceptions of species' threats and population trends to inform conservation efforts: the Bornean orangutan case study. *Diversity and Distributions* 21, 487-499. 10.1111/ddi.12286.
11. Rijksen, H.D., and Meijaard, E. (1999). Our vanishing relative. The status of wild orangutans at the close of the twentieth century (Kluwer Academic Publishers).
12. Morgans, C.L., Santika, T., Meijaard, E., Ancrenaz, M., and Wilson, K.A. (2019). Cost-benefit based prioritisation of orangutan conservation actions in Indonesian Borneo. *Biological Conservation* 238, 108236. 10.1016/j.biocon.2019.108236.

13. Wilson, H., Meijaard, E., Venter, O., Ancrenaz, M., and Possingham, H.P. (2014). Conservation Strategies for Orangutans: Reintroduction versus Habitat Preservation and the Benefits of Sustainably Logged Forest PLOS ONE 9, e102174. 10.1371/journal.pone.0102174.
14. Chua, L., Harrison, M., Cheyne, S., Fair, H., Milne, S., Palmer, A., Rubis, J., Thung, P., Wich, S., Büscher, B., et al. (2020). Conservation and the social sciences: beyond critique and co-optation. A case study from orangutan conservation. People Nat. 2, 42-60. 10.1002/pan3.10072.
15. Gaveau, D.L.A., Sheil, D., Husnayaen, M., Salim, A., Ancrenaz, M., Pacheco, P., and Meijaard, E. (2016). Rapid conversions and avoided deforestation: examining four decades of industrial plantation expansion in Borneo. Sc. Rep. 6, 32017. 10.1038/srep32017.
16. Santika, T., Wilson, K.A., Law, E.A., St John, F.A.V., Carlson, K.M., Gibbs, H., Morgans, C.L., Ancrenaz, M., Meijaard, E., and Struebig, M.J. (2021). Impact of palm oil sustainability certification on village well-being and poverty in Indonesia. Nature Sustainability 4, 109-119. 10.1038/s41893-020-00630-1.
17. Ancrenaz, M., Oram, F., Nardiyono, Silmi, M., Jopony, M.E.M., Voigt, M., Seaman, D.J.I., Sherman, J., Lackman, I., Traeholt, C., et al. (2021). Importance of orangutans in small fragments for maintaining metapopulation dynamics. Frontiers in Forests and Global Change 4, 560944. 10.3389/ffgc.2021.560944
18. Sherman, J., Ancrenaz, M., and Meijaard, E. (2020). Shifting apes: Conservation and welfare outcomes of Bornean orangutan rescue and release in Kalimantan, Indonesia. Journal for Nature Conservation 55, 125807. 10.1016/j.jnc.2020.125807.
19. Chua, L., Fair, H., Schreer, V., StEPIeN, A., and Thung, P.H. (2021). "Only the orangutans get a life jacket". American Ethnologist n/a. <https://doi.org/10.1111/amet.13045>.
20. Santika, T., Kusworo, A., Hutabarat, J.A., Sulhani, Trison, S., Raharjo, S., Ekaputri, A.D., Stigner, M., Huda, I., Meijaard, E., et al. (2017). Community forest management in Indonesia: Avoided deforestation in the context of anthropogenic and climate complexities. Glob. Env. Ch. 46 60–71. 10.1016/j.gloenvcha.2017.08.002.
21. Yuliani, E.L., Adnan, H., Achdiawan, R., Bakara, D., Heri, V., Sammy, J., Salim, M.A., and Sunderland, T. (2018). The roles of traditional knowledge systems in orang-utan Pongo spp. and forest conservation: a case study of Danau Sentarum, West Kalimantan, Indonesia. Oryx 52, 156-165. 10.1017/S0030605316000636.
22. Merten, J., Nielsen, J.Ø., Rosyani, Soetarto, E., and Faust, H. (2021). From rising water to floods: Disentangling the production of flooding as a hazard in Sumatra, Indonesia. Geoforum 118, 56-65. 10.1016/j.geoforum.2020.11.005.
23. Sabah Wildlife Department (2020). Orang-utan Action Plan. Sabah Wildlife Department.
24. Bryan, J.E., Shearman, P.L., Asner, G.P., Knapp, D.E., Aoro, G., and Lokes, B. (2013). Extreme Differences in Forest Degradation in Borneo: Comparing Practices in Sarawak, Sabah, and Brunei. PLoS ONE 8, e69679. 10.1371/journal.pone.0069679.

- 800 25. Tran, V.T. (2013). The middle-income trap: Issues for members of the Association of
801 Southeast Asian Nations. ADBI Working Paper 421. Available at:
802 <https://ssrn.com/abstract=2266239>.
- 803 26. Woo, W.T., and Hong, C. (2010). Indonesia's economic performance in comparative
804 perspective and a new policy framework for 2049. *Bulletin of Indonesian Economic*
805 *Studies* 46, 33-64. 10.1080/00074911003642237.
- 806 27. Ferraro, P.J. (2009). Counterfactual thinking and impact evaluation in environmental
807 policy. In *Environmental program and policy evaluation. New Directions for Evaluation*
808 M. Birnbaum, and P. Mickwitz, eds. pp. 75–84. 10.1002/ev.297.
- 809 28. Singleton, I., and van Schaik, C.P. (2001). Orangutan Home Range Size and Its
810 Determinants in a Sumatran Swamp Forest. *International Journal of Primatology* 22, 877-
811 911. 10.1023/a:1012033919441.
- 812 29. Suhirman, Alamsyah, Z., Zaini, A., Sulaiman, and Nikoyan, A. (2012). Studi Perencanaan
813 dan Penganggaran Bagi Pengelolaan Hutan Berbasis Masyarakat di Indonesia. *Kemitraan*.
- 814 30. FSC. (2000). FSC Principles and Criteria. Document 1.2 (Forest Stewardship Council).
- 815 31. RSPO (2018). RSPO Principles & Criteria Certification For the Production of Sustainable
816 Palm Oil. 2018. Roundtable on Sustainable Palm Oil.
- 817 32. Conservation Measures Partnerships (2016). Conservation Action Classification 2.0.
818 Available at: <https://www.ccneglobal.com/resource/8i/>.
- 819 33. Junker, J., Kühl, H.S., Orth, L., Smith, R.K., Petrovan, S.O., and Sutherland, W.J. (2019).
820 Primate conservation. In *What Works in Conservation*, W.J. Sutherland, L.V. Dicks, N.
821 Ockendon, S.O. Petrovan, and R.K. Smith, eds. (Open Book Publishers), pp. 439-492.
- 822 34. Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., and
823 Lackman, I. (2010). Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia,
824 show that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. *PloSOne*
825 5, e11510. doi:11510.11371/journal.pone.0011510.
- 826 35. Meijaard, E., Mengersen, K., Buchori, D., Nurcahyo, A., Ancrenaz, M., Wich, S., Atmoko,
827 S.S.U., Tjiu, A., Prasetyo, D., Nardiyono, et al. (2011). Why don't we ask? A
828 complementary method for assessing the status of great apes. *PloS ONE* 6, e18008.
829 10.1371/journal.pone.0018008.
- 830 36. Lakner, C., Mahler, D.G., Nguyen, M.C., Azevedo, J.P., Chen, S., Jolliffe, D.M., Prydz,
831 E.B., and Sangraula, P. (2018). Consumer Price Indices used in Global Poverty
832 Measurement. World Bank Group Global Poverty Monitoring Technical Note No. 4. The
833 World Bank.
- 834 37. Ridgeway, G. (2007). Generalized Boosted Models: A guide to the gbm package (R
835 Foundation for Statistical Computing).
- 836 38. Austin, K.G., Schwantes, A., Gu, Y., and Kasibhatla, P.S. (2019). What causes
837 deforestation in Indonesia? *Environmental Research Letters* 14, 024007. 10.1088/1748-
838 9326/aaf6db.

- 839 39. Russon, A.E. (2009). Orangutan rehabilitation and reintroduction. In *Orangutans.*
840 *Geographic variation in behavioral ecology and conservation*, S. Wich, S.U. Atmoko, T.M.
841 Setia, and C.P. van Schaik, eds. (Oxford University Press), pp. 327-350.
842 10.1093/acprof:oso/9780199213276.003.0023.
- 843 40. Yayasan Ekosistem Lestari (2018). YEL Annual Report 2017. Yayasan Ekosistem Lestari.
844

Key resources table

Deposited data		
Orangutan conservation investment data	This paper, Table S1 and S2	http://apesportal.eva.mpg.de/database/archiveTable (this database is being moved; an updated location will be provided prior to publication)
Orangutan nest surveys 2015-2019	This paper	http://apesportal.eva.mpg.de/database/archiveTable (this database is being moved; an updated location will be provided prior to publication)
Orangutan or nest encounters and reconnaissance surveys 2015-2019	This paper	http://apesportal.eva.mpg.de/database/archiveTable (this database is being moved; an updated location will be provided prior to publication)
Sightings of orangutans reported by village residents through interviews 2015-2019	This paper	http://apesportal.eva.mpg.de/database/archiveTable (this database is being moved; an updated location will be provided prior to publication)

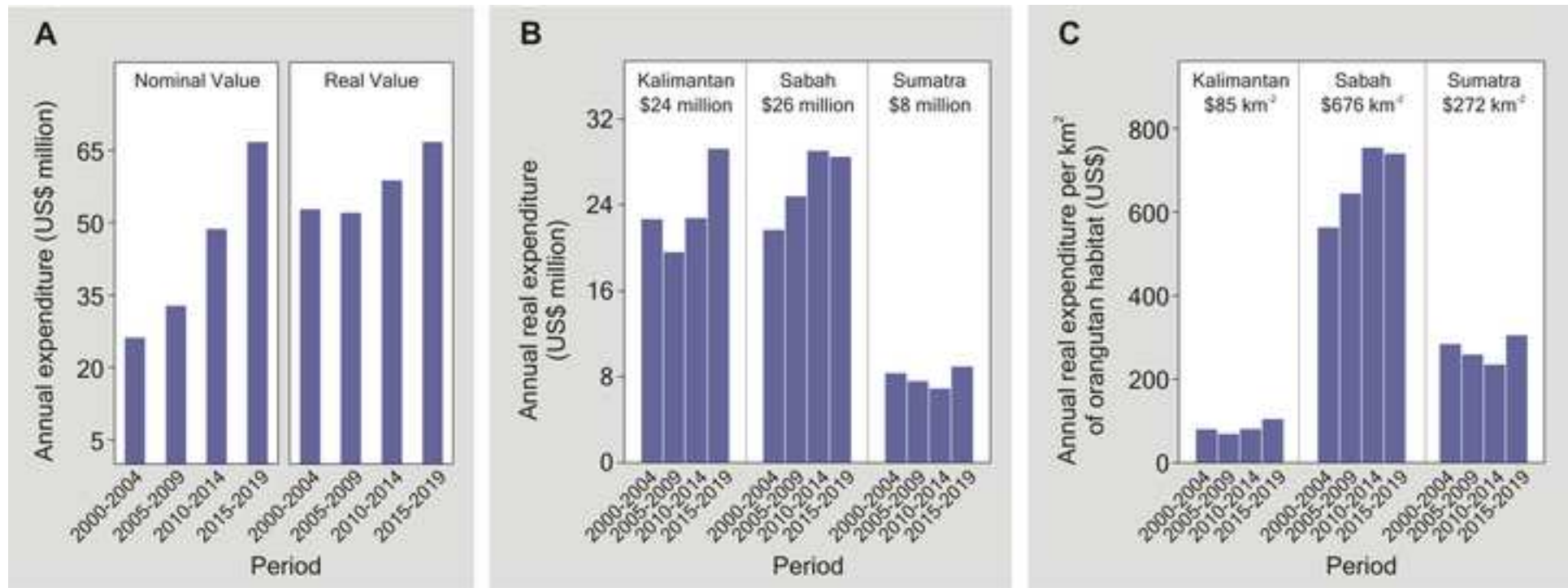
Orangutan survey data from 2000 to 2015	5, 4, 2	http://apesportal.eva.mpg.de/datab ase/archiveTable (this database is being moved; an updated location will be provided prior to publication)
Elevation (m a.s.l) <i>ELEV</i>	SRTM 90m Digital Elevation Database v4.1 ⁷ ³⁷	https://cg iarcsi.community/data/srt m-90m-digital-elevation-database-v4-1/
Rainfall during the dry season (mm) <i>SDRY</i>	WorldClim2 ³⁸	https://www.worldclim.org/data/bi oclim.html ; BIO17
Rainfall during the wet season (mm) <i>SWET</i>	WorldClim2 ³⁸	https://www.worldclim.org/data/bi oclim.html ; BIO16
Distance to nearest city (km) <i>CITY</i>	Provincial map from the Geospatial Information Agency Indonesia ³⁹ and GeoNames Gazetteer ⁴⁰	http://www.geonames.org/ https://tanahair.indonesia.go.id/por tal-web
Percentage of peatland area <i>PEAT</i>	Peat hydrological area map ⁴¹	http://pkgppkl.menlhk.go.id/v0/en/ kesatuan-hidrologis-gambut-nasional-skala-1250-000/
Percent forest cover <i>FOREST</i>	Global Forest Change dataset ⁴² , Indonesia's primary and secondary forest map ⁴³ , and Intact Forest Landscapes data ⁴⁴	https://earthenginepartners.appspot .com/science-2013-global-forest/download_v1.7.html https://glad.umd.edu/dataset/prima ry-forest-cover-loss-indonesia-2000-2012

Percentage of degraded peatland <i>DEGPT</i>	Peat hydrological area map ⁴¹ , Global Forest Change dataset ⁴² , Indonesia's primary and secondary forest map ⁴³ , and Intact Forest Landscapes data ⁴⁴	https://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.7.html https://glad.umd.edu/dataset/primary-forest-cover-loss-indonesia-2000-2012 http://pkgppkl.menlhk.go.id/v0/en/kesatuan-hidrologis-gambut-nasional-skala-1250-000/
Distance to oil palm plantations (km) <i>OPDST</i>	Oil palm plantation distribution map ^{16,45-47}	www.cifor.org/map/atlas
Survey effort <i>SURV</i>	Orangutan survey datasets across Indonesia and Malaysia ^{2,5,17,31,32}	See row 5, this table
Distance to research centres/activities (km) <i>RSCHR</i>	This paper	See Table S1
Distance to protected areas (km) <i>PRTCA</i>	Forest Zone Maps ^{5,48} Community Forestry areas ⁴⁹ and this paper	http://webgis.dephut.go.id:8080/ke-menhut/index.php/id/peta/petapiaps , and Table S1
Distance to patrolling activities (km) <i>PTROL</i>	This paper	See Table S1
Distance to rehabilitation centres (km) <i>RHCTR</i>	This paper	See Table S1
Distance to reintroduction sites (km) <i>RINTR</i>	This paper	See Table S1
Distance to public outreach programs (km) <i>COMRC</i>	This paper	See Table S1
Experimental models: Organisms/strains		

Bornean orangutan (<i>Pongo pygmaeus</i>)	NA	NA
Sumatran orangutan (<i>Pongo abei</i>)	NA	NA
Tapanuli orangutan (<i>Pongo tapanuliensis</i>)	NA	NA
Software and algorithms		
R software		https://www.r-project.org/
R code		DOI to repository will be made available
Arc-GIS		https://www.arcgis.com/index.html
Other		
Computation of inflation adjusted investment	This paper	See Method Details
Computation of counterfactuals	This paper	See Method Details
Computation of cost effectiveness	This paper	See Method Details

Figure 1





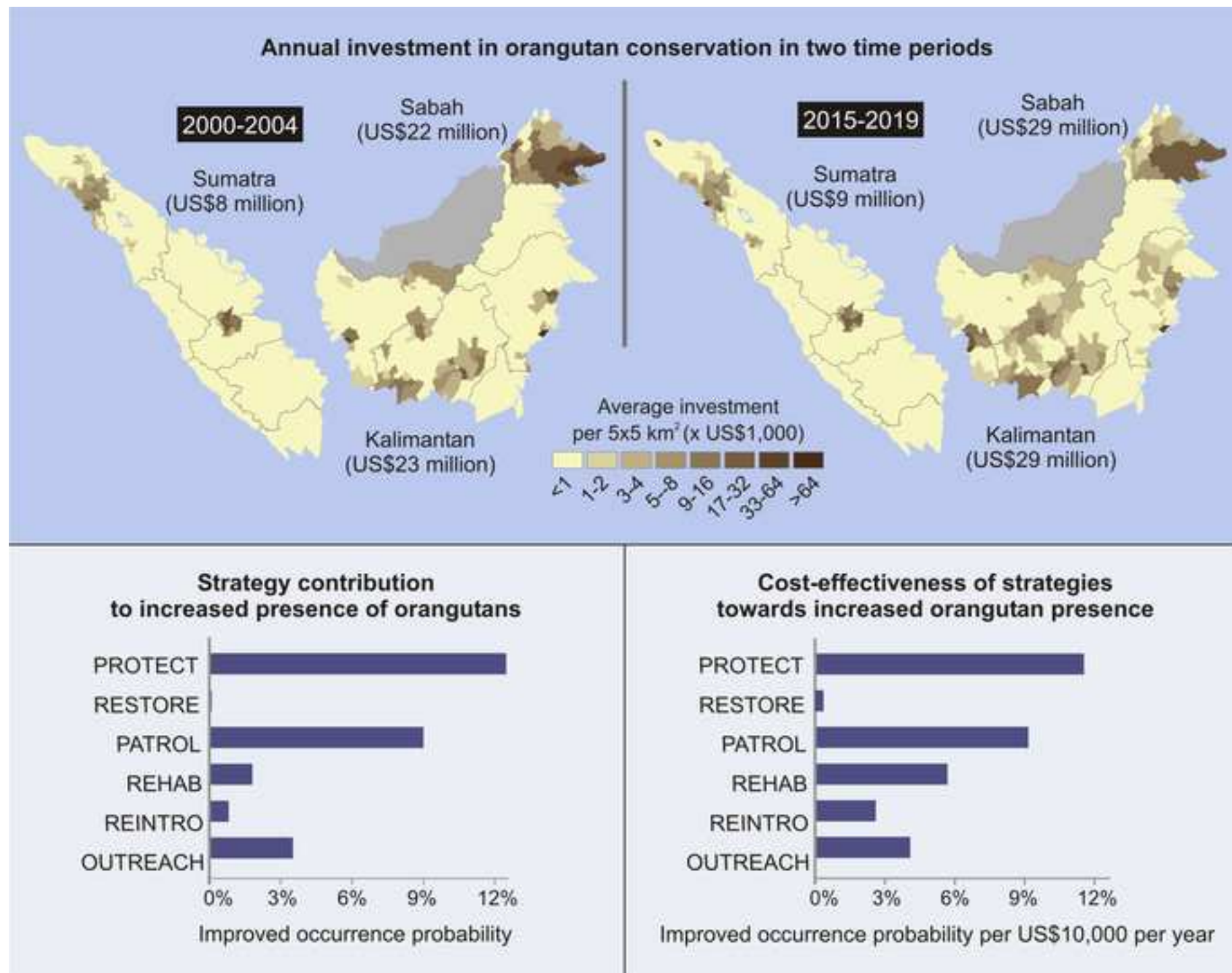
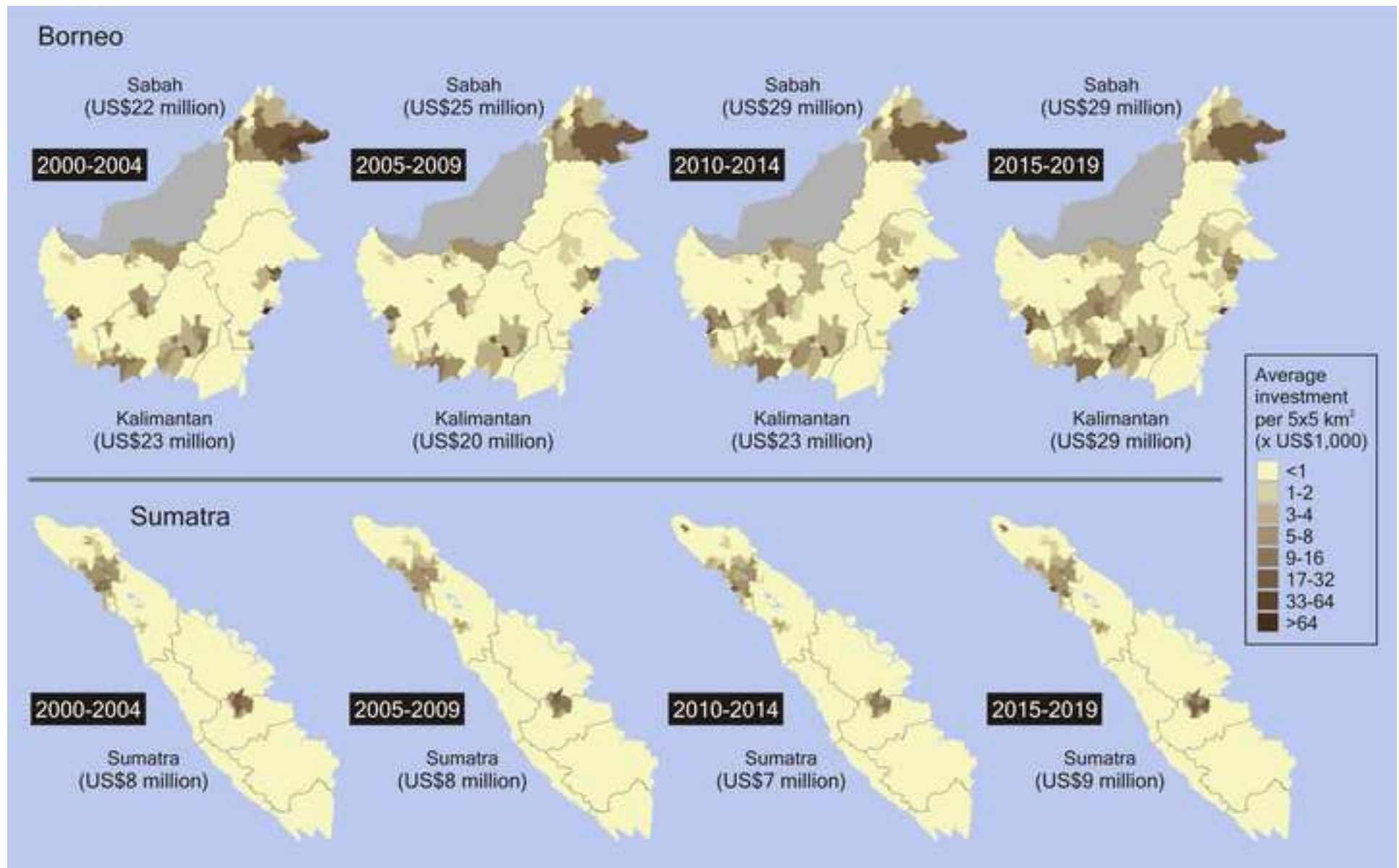
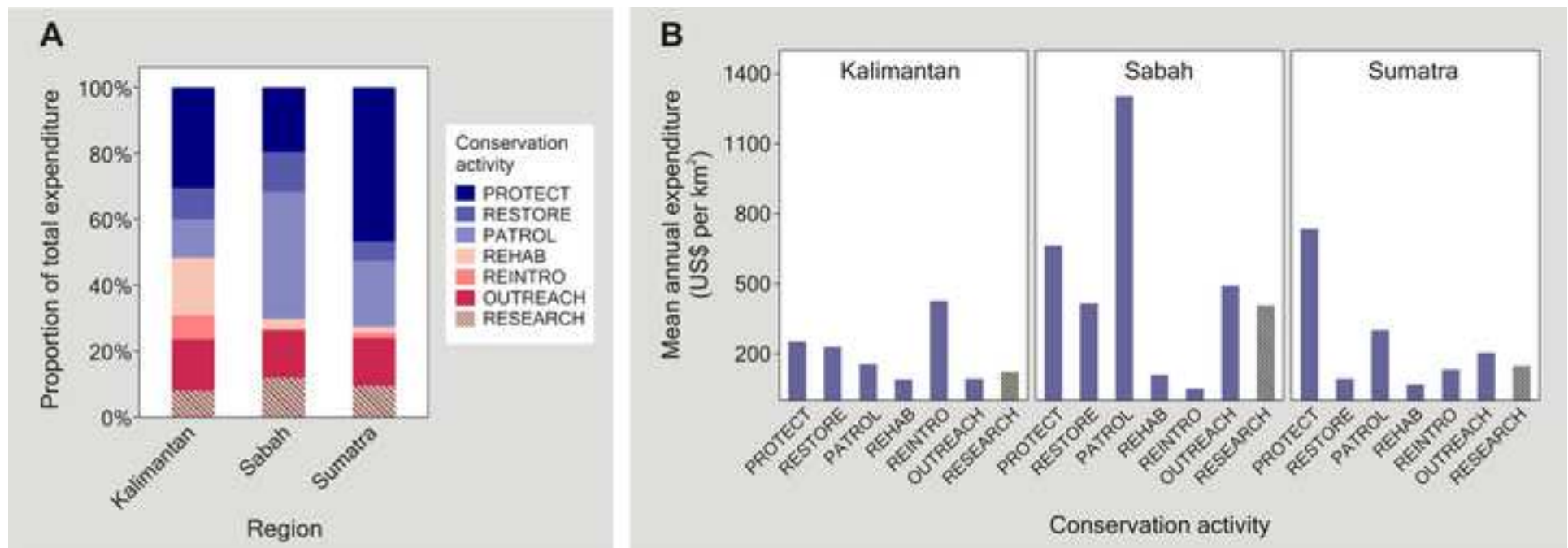
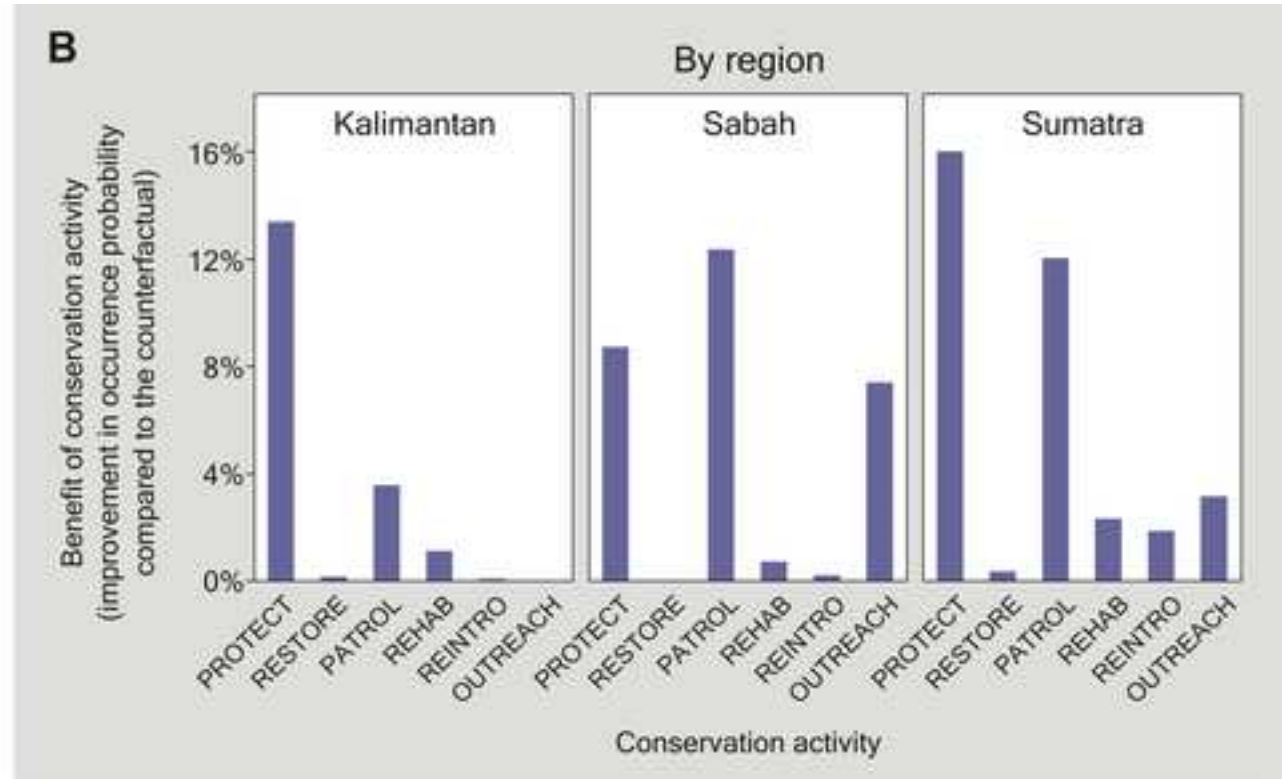
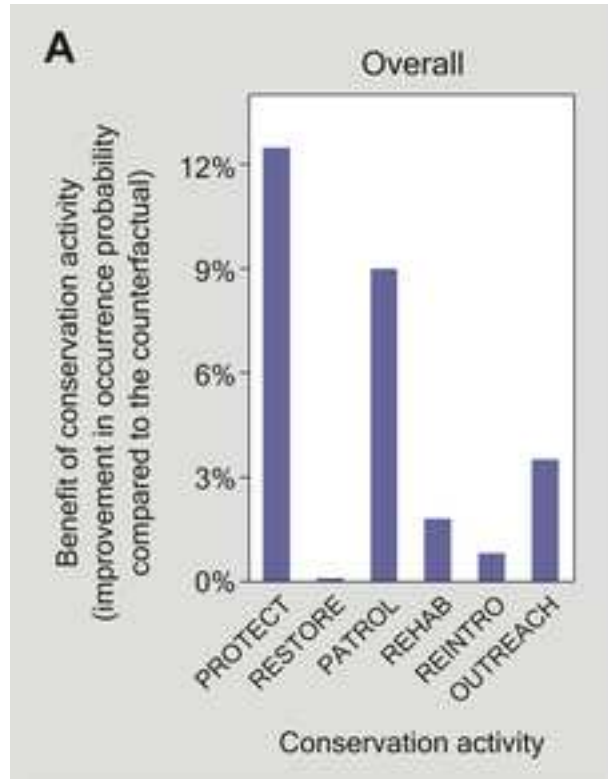
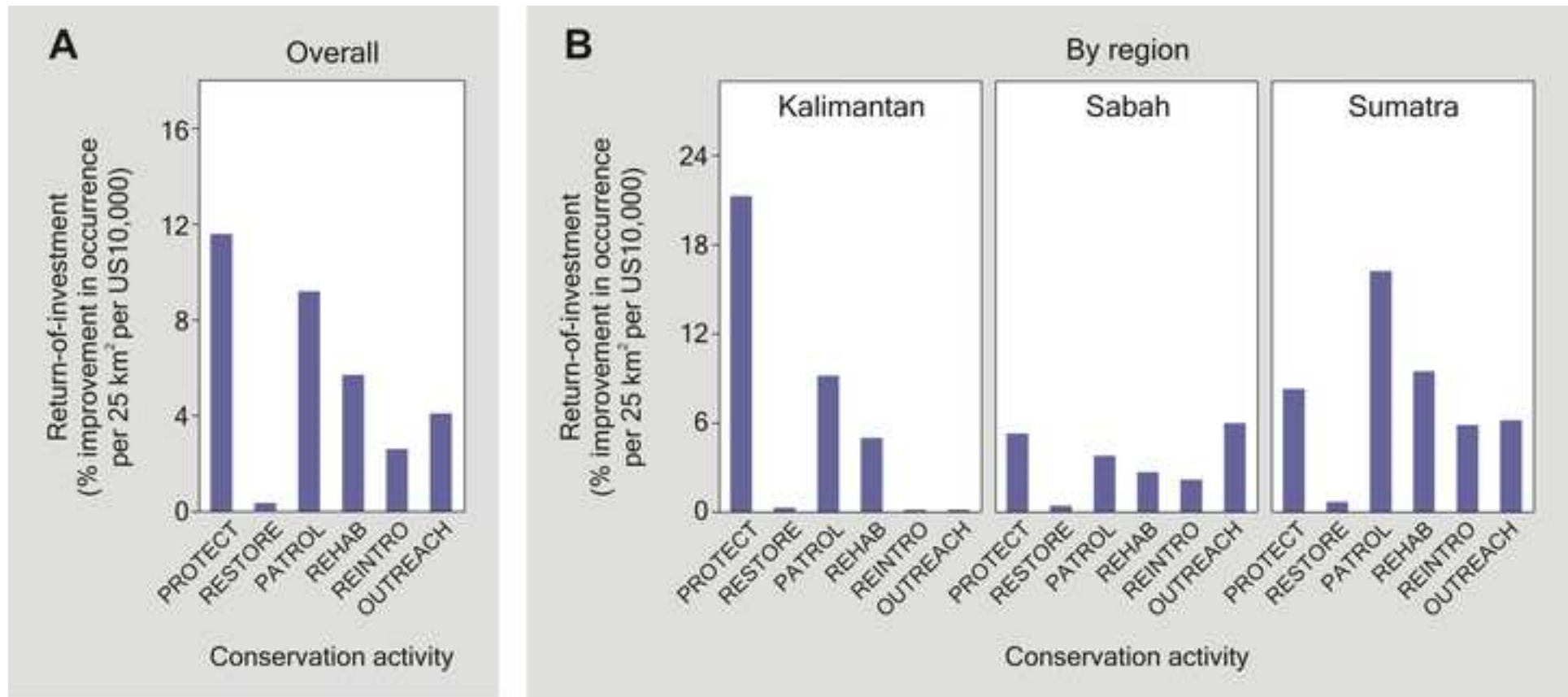


Figure 3









Figures

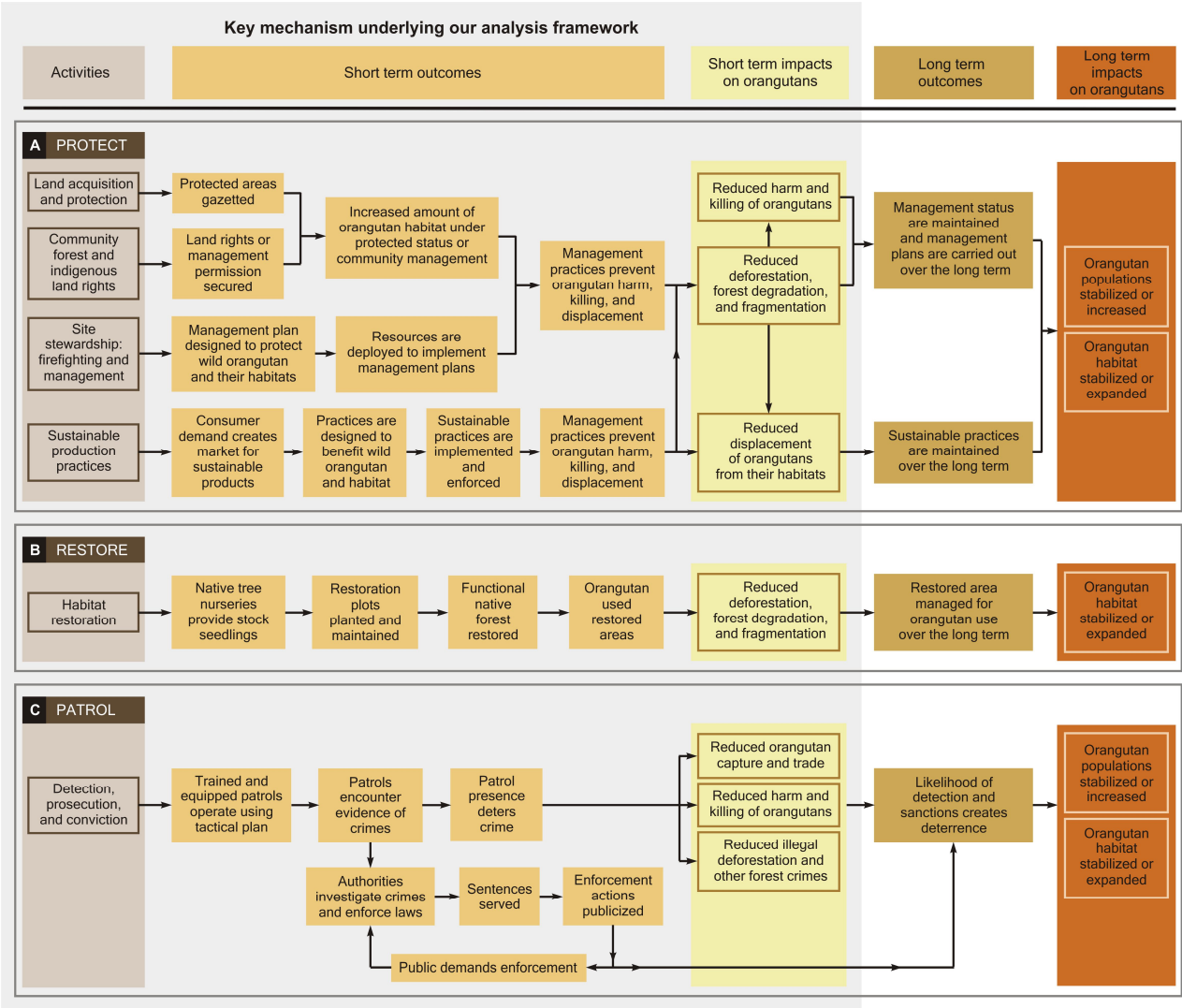


Figure S1. Orangutan conservation Theory of Change (ToC) pathways for protection, restoration and patrolling. Related to STAR Methods.

(a) PROTECT, (b) RESTORE, and (c) PATROL. The pathways represent the sequential outcomes possible from the conservation activity over the short term (within five years after the action is initiated) and long term (more than five years), and how these outcomes can lead to reduced threats and positive impacts for the species. Our study focuses on the short-term implications of the orangutan conservation activities (in grey background). Explanations of the ToC pathways are provided in the Data.

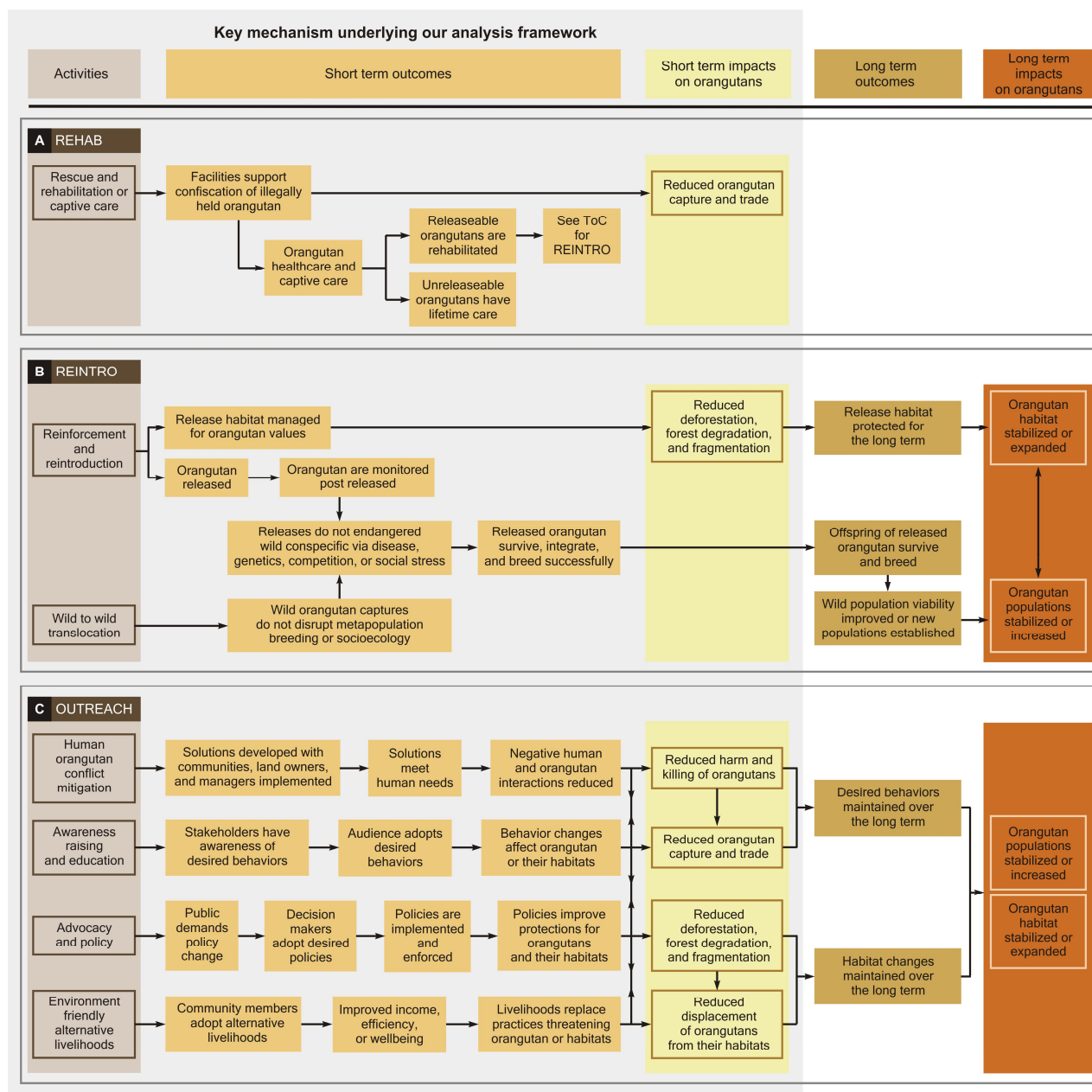


Figure S2. Orangutan conservation Theory of Change (ToC) pathways for rehabilitation, reintroduction and outreach. Related to STAR Methods.

(a) REHAB, (b) REINTRO, and (c) OUTREACH. The pathways represent the sequential outcomes possible from the conservation activity over the short term (within five years after the action is initiated) and long term (more than five years), and how these outcomes can lead to reduced threats and positive impacts for the species. Our study focuses on the short-term implication of the orangutan conservation activities (in grey background). Explanations of the ToC pathways are provided in the Data.

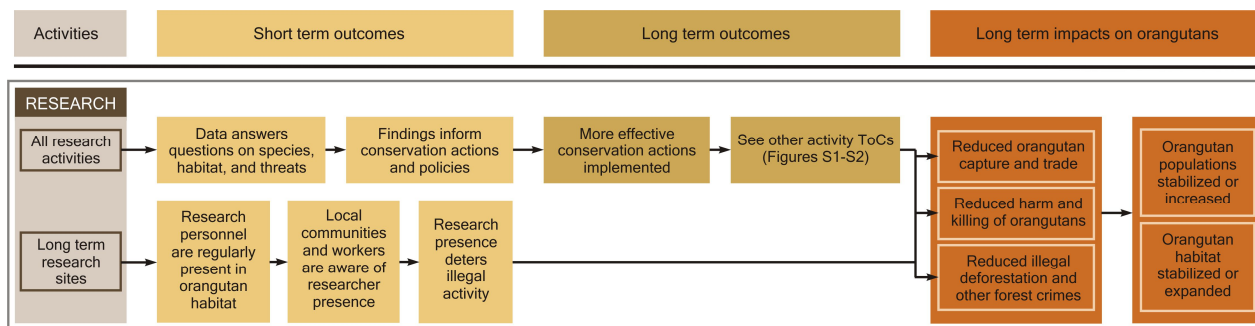


Figure S3. Theory of Change (ToC) pathways for orangutan related RESEARCH activity. Related to STAR Methods.

This represents the chain of outcomes possible from the activity within the short term (five years) and long term (beyond five years).

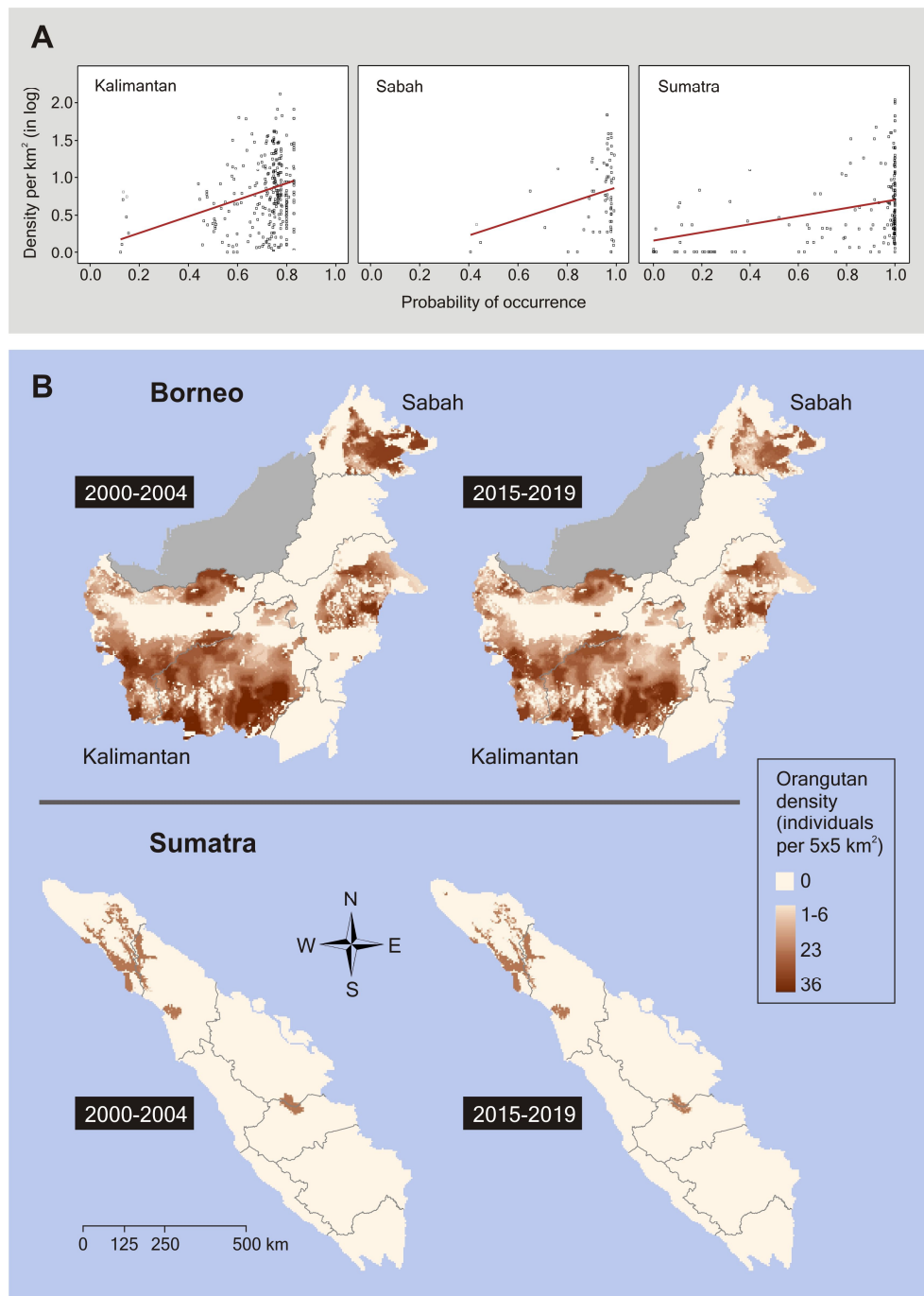


Figure S4. The relationship between probability of occurrence and density and density change over time. Related to STAR Methods and Figure 5.

(A) The relationship between the orangutan probability of occurrence and density for the three study regions. Occurrence data were generated from the Generalized Boosted Regression Models – GBM. Density was estimated from the transect dataset. (B) Estimated change in density of orangutan populations between 2000-2004 and 2015-2019. Borneo and Sumatra. Three regional-based models were used to estimate the change in orangutan distributions in (1) Kalimantan and (2) Sabah, and (3) Sumatra.

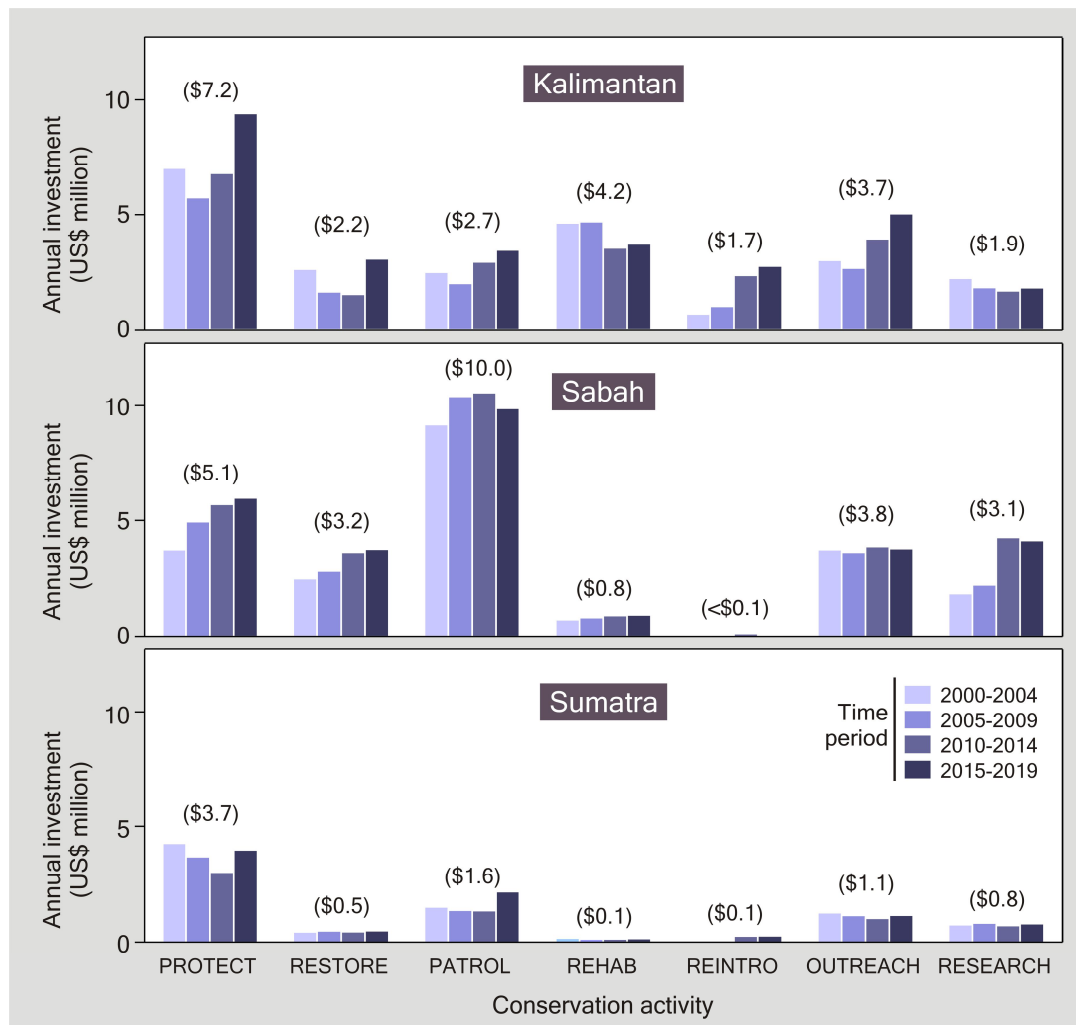


Figure S5. Annual spending value on different conservation activities for the orangutan in Kalimantan, Sabah, and Sumatra over time. Related to Figure 4.

Conservation activities assessed include the six core activities considered affecting the orangutan survival in the short term: habitat acquisition and protection (PROTECT), habitat restoration (RESTORE), patrolling and law enforcement (PATROL), rescue and rehabilitation (REHAB), translocation and reintroduction (REINTRO), and public outreach and capacity building (OUTREACH); and research-related activities considered as primarily influencing conservation actions and land use management decisions (RESEARCH). The value inside the parenthesis represents the mean annual investment value between 2000 and 2019 for the associated action (in million US\$).

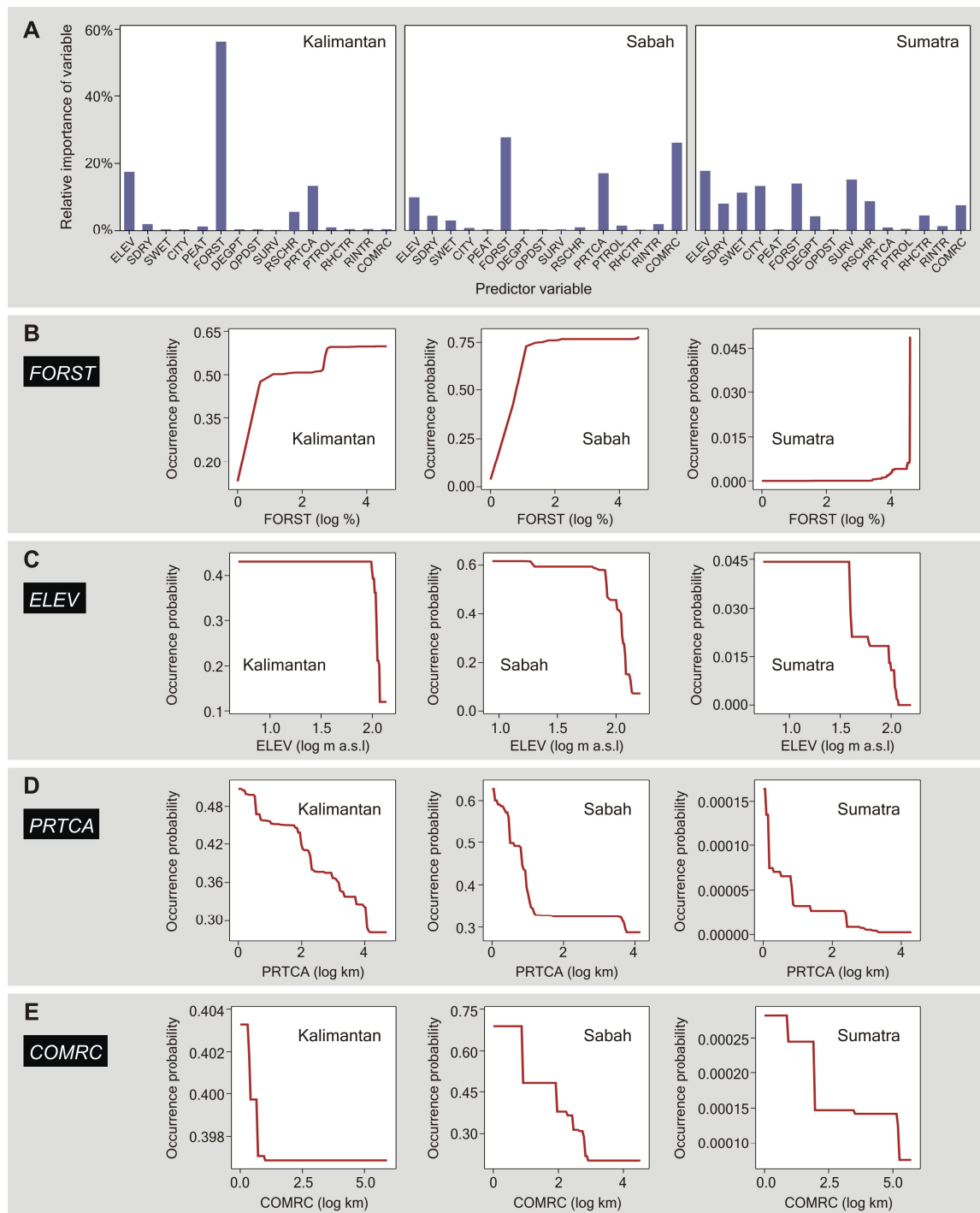


Figure S6. Predictors of orangutan occurrence. Related to STAR Methods.

(A) The relative importance of environmental predictors in affecting orangutan likelihood of occurrence, and the marginal effects of predictors with high importance obtained from the three region-based GBM models for Kalimantan, Sabah, and Sumatra, including variables: (B) forest cover (*FORST*), (C) elevation (*ELEV*), (D) distance to protected areas (*PRTCA*), and (E) distance to public outreach and awareness raising programs (*COMRC*). Survey effort had a negligible effect on the likelihood of orangutan reported as presence in Kalimantan and Sabah, but in Sumatra it had a large positive association with orangutan presences (A). Forest cover and elevation are the strongest predictors of orangutan distributions in the three islands (A). The species' probability of occurrence increases with increased forest cover and reduced elevation (B-C). In Kalimantan and Sabah, proximity to protected areas has a strong positive correlation with orangutan distributions (D). In Sabah, the probability of orangutan occurrence also markedly increases with proximity to community outreach programs (E).

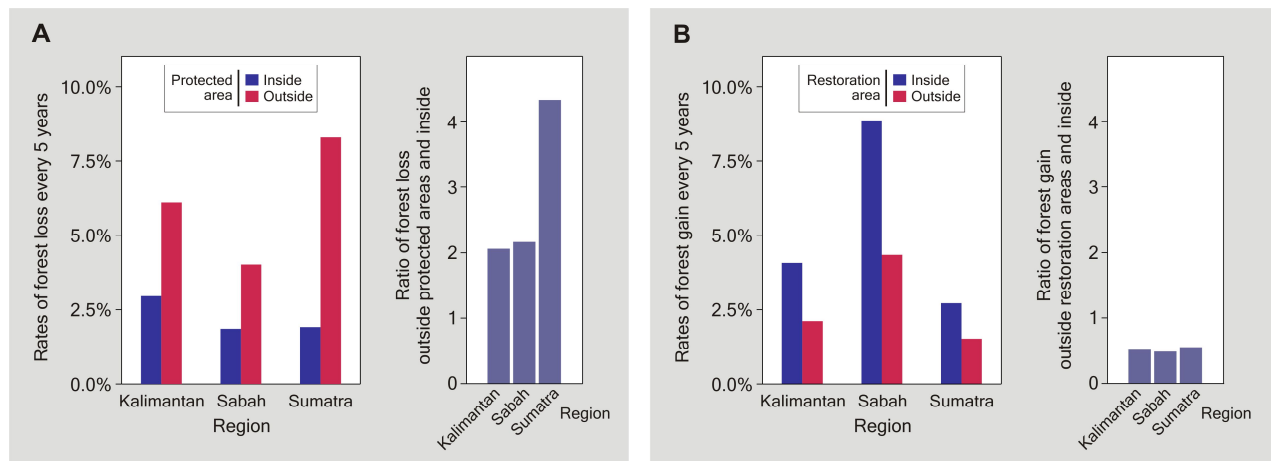


Figure S7. Forest gain and loss data used in counterfactual analysis. Related to STAR Methods.

Rates of (A) forest loss inside protected areas compared to the rates within a 50 km buffer zone, and (B) forest gain inside restoration sites compared to the rates within a 50 km buffer zone, every five years between 2000 and 2019 in Kalimantan, Sabah, and Sumatra.

Tables

Published and unpublished datasets	
United States Fish and Wildlife Service (USFWS) Multinational Species Conservation Fund - Great Apes grants to orangutan projects (data provided by USFWS)	
Dataset of oil palm companies operating in orangutan habitat ^{S1}	
Borneo Atlas (https://atlas.cifor.org/borneo/#en)	
Dataset of rescue centers operating in Borneo	
Websites	
Site	Search terms
United States Agency for International Development (USAID) LESTARI program (https://www.lestari-indonesia.org/en/)	
Tropical Forest Conservation Act (TFCA) Sumatra annual reports (http://tfcasumatera.org/publikasi_category/laporan-tahunan/)	
TFCA Kalimantan annual reports (https://www.tfcakalimantan.org/kanal/annual-report)	
European Union (EU) Commission funded projects by country (https://ec.europa.eu/budget/euprojects/search-projects_en)	
Critical Ecosystem Partnership Fund (https://www.cepf.net/grants/grantee-projects)	Taxon: “mammals”; Country: “Indonesia” and “Malaysia”
The Global Environmental Facility (GEF) project database (https://www.thegef.org/projects)	“Indonesia” and “Malaysia”
Mohammed bin Zayed Species Conservation Fund projects (https://www.speciesconservation.org/case-studies-projects/)	Species: “mammals”; Continent: “Asia”; Country: “Indonesia” and “Malaysia”
Darwin Initiative projects (https://www.darwininitiative.org.uk/project/)	Location; Country: “Indonesia” and “Malaysia”
Norway bilateral projects in Indonesia (https://www.norway.no/en/indonesia/values-priorities/deforestation-and-climate-change/bilateral-climate-and-forest-support/project-support/)	
Australian Agency for International Development (https://dfat.gov.au/geo/indonesia/development-assistance/Pages/development-assistance-in-indonesia.aspx)	
Japan International Cooperation Agency (https://www.jica.go.jp/indonesia/english/index.html and https://www.jica.go.jp/malaysia/english/index.html)	
Agence Française de Développement (https://www.afd.fr/en/page-region-pays/indonesia)	
Deutsche Gesellschaft für Internationale Zusammenarbeit (GIZ) (https://www.giz.de/en/html/about_giz.html)	Worldwide: “Indonesia” and “Malaysia”
Partnerships for Forests – Our Portfolio (https://partnershipsforforests.com/what-we-do/partnerships-and-projects/)	Location: “Indonesia”
The Arcus Foundation grantees (https://www.arcusfoundation.org/grantees/)	Focus: “Great apes and gibbons”
Prince Bernhard Nature Fund (https://www.pbnf.nl/projects/)	“Indonesia” and “Malaysia”
Search engines	
Site	Search terms
Foundation Directory Online	Keywords: “orangutan”, “orang utan” and “orang-utan”

Table S1. Sources used to identify additional investments in orangutan conservation. Related to Key Resources Table, STAR Methods.

<p>Organizations operating across all orangutan habitats: IUCN SGA; UNEP; GRASP; Great Apes Film Initiative; Orangutan Conservancy; Yayasan Kehutanan Masyarakat Indonesia; Yayasan Swara Owa; Yayasan Ulos Heritage Indonesia (SCORPION); FORINA; CIFOR; University of Kent DICE; Borneo Futures; Wildlife Impact.</p>
<p>Organizations operating in Indonesian Kalimantan: ADB/GEF-funded project (Sustainable Forest and Biodiversity Management in Borneo); UNEP/Wetlands International Indonesia/Global Environmental Centre; Canadian Government (CIDA); UNDP – Kalimantan; Indonesian International Rural Agricultural Development Foundation; Kalimantan Prima Coal; Agro Bukit (Goodhope Holdings); Agro Wana Lestari (Goodhope Holdings); Dewata Sawit Nusantara (DSN group); Genting – Kalimantan; Globalindo Alam Perkasa (Musim Mas); Harapan Sawit Lestari; Investa Karya Bhakti; Karya Makmur Bahagia; Karya Makmur Sejahtera (Goodhope Holdings); Kridatama Lancar (Sime Darby); Mentaya Sawit Mas (Wilmar); Nabatindo Karya Utama (Bumitama); Kalimantan Agro Lestari; Rea Kaltim Plantation; Sarana Titian Permata (Wilmar); Sawit Sumber Mas Sarana; Sinar Mas – GAR; Sukajadi Sawit Mekar (Musim Mas); Swakarsa Sinar Sentosa (Sinar Mas); Tapian Nadenggan (Sinar Mas); Makin Group; Katingan Mentaya Project; Rimba Raya Restoration Ecosystem; Acacia Andalan Utama; Balayan River Timber; Bina Ovivipari Semesta; Carus Indonesia; Djima Jaya Utama; Erna Djuliawati; Graha Sentosa Permai; Gunung Gajah Abadi; Karya Lestari; Narkata Timber; Royal Lestari Utama; Saratim (Sarmiento Parakantja Timber); Sari Bumi Kusuma; Suka Jaya Makmur; Utama Damai Indah Timber; Wanasokan Hasilindo; Balai Konservasi Sumber Daya Alam Kalbar; Balai Konservasi Sumber Daya Alam Kalteng; Balai Konservasi Sumber Daya Alam Kaltim; Danau Sentarum and Betung Kerihun National Park; Gunung Palung National Park; Bukit Baka/Bukit Raya National Park; Tanjung Puting National Park; Sebangau National Park; Kutai National Park; Badan Restorasi Gambut (Peat Restoration Agency); Aidenvironment; Borneo Nature Foundation; CAN Borneo; FFI Indonesia; Friends of the National Parks Foundation; IDH Ketapang landscape; Integrated Conservation; Link-AR Borneo; People Resources and Conservation Foundation (PRCF); Planet Indonesia; Profauna; Save Our Borneo; TNC Indonesia; WALHI Indonesia; WCS Indonesia – Kalimantan; Wetlands International Indonesia; YTS/Wildlife Impact – community surveys; World Education – Indonesia; WWF Indonesia; Yayasan; Brunel University; CIMPTROP - University of Palangka; Wallacea Trust; Yayasan TITIAN; Gunung Palung Orangutan Conservation; Health in Harmony; Kutai Project; Mohammed bin Zayed Conservation Fund – in situ research funds, Kalimantan; Orangutan Land Trust; Tropenbos-International; Tuanan Orangutan Research Project/CORE Borneo; University College Birmingham – in situ research Kalimantan; BOSF Nyaru Menteng; Wanasokan Samboja/Samboja Lestari, Mawas; RHO/BOSF; Center for Orangutan Protection; International Animal Rescue; Jakarta Animal Aid Network; Jejak Puleng; Orangutan Foundation UK; Orangutan Foundation International; Sintang Orangutan Centre; Tenggara rescue/transfer facility.</p>
<p>Organizations operating in Malaysian Sabah: Anika Desiran; Deramakot Forest Reserve; INIKEA; Mayvin Grouping; PONGO Alliance; Sapulut; TSH Resources - natural forest management; TSH Resources -oil palm; Yayasan Sabah; Linbar 1 and 2 Estates; Litang Estate; Santosa Estate (Sime); Sg. Pin Estate; Sungai Segama II; Tabin Estate; Tagas Estate; Sabah Softwoods; Tungku Estate (Sime); Wilmar - Sabah Mas estate (Tabin) (excluding PONGO Alliance); Genting; Sabah Environmental Protection; Sabah Forestry Department; Sabah Parks; UE - REDD+; UNDP; Borneo Conservation Trust – Japan; Borneo Conservation Trust – Sabah; Ecohealth Alliance; Friends of the Orangutan (FOTO); HUTAN-KOCP; HUTAN - via Wildlife Connection; LEAP; Malaysia Palm Oil Wildlife Conservation Fund; Orangutan Appeal-UK (Sabah); Orangutan Appeal-UK (Sabah Wildlife Rescue Unit); Rhino and Forest Fund; PACOS; Rainforest Trust/SEARRP; Sabah Environmental Protection Association; WWF-Sabah; WWF-Sabah Living Landscapes; Danau Girang Field Center; Durrell Trust for Conservation; Liverpool John Moores University; Living Landscape Alliance; Orangutan Appeal-UK (Sabah – tabin PRM project); SEARRP - SAFE Project; Yayasan Sime Darby; Sepilok.</p>
<p>Organizations operating in Indonesian Sumatra: UNDP; TFCA/Leuser Conservation Partnership; Asia Pacific Resources International Limited (APRIL); Royal Lestari Utama; North Sumatra Hydroelectric Company; Balai Konservasi Sumber Daya Alam Sumatera Utara; Balai Konservasi Sumber Daya Alam Sumatera Jambi; Gunung Leuser National Park; Bukit Tigapuluh National Park; Conservation International Indonesia; FKL; Frankfurt Zoological Society; HAKA; INDECON; Institute Green Aceh (IGA); Jantho Lestari Consortium; Lembaga Suar Galang Keadilan; Leuser Ecosystem Management Authority Employee Forum; Nature for Change; Orangutan Information Center; Orang Utan Republik/TOP; PADHI Foundation; Penyangga Tengah Kawasan Ekosistem Leuser; PETRA; Rainforest Action Network; Rainforest trust/KEHUS; Sumatra Ranger Project/Yayasan Cahaya Anak Nusantara; Sumatran Rainforest Institute/tapanuli Orangutan Conservation Project (TOCOP); Universitas Nasional (Unas) Faculty of Biology; WALHI Indonesia; WCS Indonesia – Sumatra; Wetlands International Indonesia; Yayasan Konservasi Satwa Liar Indonesia (YKSLI); Yayasan Leuser International (Leuser International Foundation, YLI); Yayasan Ulos Heritage Indonesia (SCORPION); Ketambe; FORINA (Sumatra); Soraya; Jakarta Animal Aid Network; SOCP; SKEPHI (Sekretariat Kerjasama untuk Pelestarian Hutan Indonesia; WildAid – Leuser project; Yayasan EKONA; Yayasan Perlindungan Lingkungan Hidup dan Pelestarian Alam (Yayasan Palapa); Leuser Development Project.</p>

Table S2. List of entities included in orangutan conservation investment dataset. Related to Key Resources Table, STAR Methods.

The analysis includes publicly available financial data for organizations whose names have been excluded for confidentiality reasons.

Variable	Variable abbreviation	Static/ Dynamic	Data sources
Elevation (m a.s.l)	<i>ELEV</i>	Static	SRTM 90m Digital Elevation Database v4.1 ^{S2}
Rainfall during the dry season (mm)	<i>SDRY</i>	Static	WorldClim ^{S3}
Rainfall during the wet season (mm)	<i>SWET</i>	Static	WorldClim ^{S3}
Distance to nearest city (km)	<i>CITY</i>	Static	Provincial map from the Geospatial Information Agency Indonesia S4 and GeoNames Gazetteer ^{S5}
Percentage of peatland area	<i>PEAT</i>	Static	Peat hydrological area map ^{S6}
Percent forest cover	<i>FOREST</i>	Dynamic	Global Forest Change dataset ^{S7} , Indonesia's primary and secondary forest map ^{S8} , and Intact Forest Landscapes data ^{S9}
Percentage of degraded peatland	<i>DEGPT</i>	Dynamic	Peat hydrological area map ^{S6} , Global Forest Change dataset ^{S7} , Indonesia's primary and secondary forest map ^{S8} , and Intact Forest Landscapes data ^{S9}
Distance to oil palm plantations (km)	<i>OPDST</i>	Dynamic	Oil palm plantation distribution map ^{S10-13}
Survey effort	<i>SURV</i>	Dynamic	Orangutan survey datasets across Indonesia and Malaysia ^{S14-18}
Distance to research centres/activities (km)	<i>RSCHR</i>	Dynamic	See Table 1
Distance to protected areas (km)	<i>PRTCA</i>	Dynamic	Forest Zone Maps ^{S14,19} , Community Forestry areas ^{S20}
Distance to patrolling activities (km)	<i>PTROL</i>	Dynamic	See Table 1
Distance to rehabilitation centres (km)	<i>RHCTR</i>	Dynamic	See Table 1
Distance to reintroduction sites (km)	<i>RINTR</i>	Dynamic	See Table 1
Distance to public outreach programs (km)	<i>COMRC</i>	Dynamic	See Table 1

Table S3. Environmental predictors used in the Generalized Boosted Regression Models (GBM) to generate the estimated change in orangutan distributions. Related to Key Resources Table, STAR Methods.

References

- S1. Morgans, C.L., Santika, T., Meijaard, E., Ancrenaz, M., and Wilson, K.A. (2019). Cost-benefit based prioritisation of orangutan conservation actions in Indonesian Borneo. *Biological Conservation* 238, 108236. <https://doi.org/10.1016/j.biocon.2019.108236>.
- S2. Jarvis, A., Reuter, H.I., Nelson, A., and Guevara, E. (2008). Hole-filled SRTM for the Globe Version 4.
- S3. Fick, S.E., and Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37, 4302-4315. <https://doi.org/10.1002/joc.5086>.
- S4. Geospatial Information Agency (BIG) (2016). Provincial Map. Jakarta, Indonesia.
- S5. GeoNames (2020). Gazetteer Data. Available at: <http://www.geonames.org/>.
- S6. Ministry of Environment and Forestry of Indonesia (MEF) (2017). Peat Hydrological Area Map. Jakarta.
- S7. Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., Thau, D., Stehman, S.V., Goetz, S.J., Loveland, T.R., et al. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science* 342, 850-853. 10.1126/science.1244693.
- S8. Margono, B.A., Potapov, P.V., Turubanova, S., Stolle, F., and Hansen, M.C. (2014). Primary forest cover loss in Indonesia over 2000-2012. *Nature Clim. Ch.* 4, 730-735. 10.1038/nclimate2277.
- S9. Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., and Esipova, E. (2017). The last frontiers of wilderness: Tracking loss of intact forest landscapes from 2000 to 2013. *Science Advances* 3, e1600821. 10.1126/sciadv.1600821
- S10. Morgans, C., Meijaard, E., Santika, T., Law, E., Budiharta, S., Ancrenaz, M., and Wilson, K. (2018). Evaluating the effectiveness of palm oil certification in delivering multiple sustainability objectives. *Environmental Research Letters* 13.
- S11. Santika, T., Budiharta, S., Law, E.A., Struebig, M., Ancrenaz, M., Poh, T.M., Wilson, K.A., and Meijaard, E. (2019). Does oil palm agriculture help alleviate poverty? A multidimensional counterfactual assessment of oil palm development in Indonesia. *World Development* 120, 105-117. 10.1016/j.worlddev.2019.04.012.
- S12. Gaveau, D.L.A., and Salim, A. (2019). Atlas of Deforestation and Industrial Plantations in Borneo. Center for International Forestry Research (CIFOR). Available at: www.cifor.org/map/atlas.
- S13. Santika, T., Wilson, K.A., Law, E.A., St John, F.A.V., Carlson, K.M., Gibbs, H., Morgans, C.L., Ancrenaz, M., Meijaard, E., and Struebig, M.J. (2021). Impact of palm oil sustainability certification on village well-being and poverty in Indonesia. *Nature Sustainability* 4, 109-119. 10.1038/s41893-020-00630-1.
- S14. Santika, T., Ancrenaz, M., Wilson, K.A., Spehar, S., Abram, N., Banes, G.L., Campbell-Smith, G., Curran, L., d'Arcy, L., Delgado, R.A., et al. (2017). First integrative trend analysis for a great ape species in Borneo. *Sc. Rep.* 7, 4839. 10.1038/s41598-017-04435-9.
- S15. Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., and Lackman, I. (2010). Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show that orang-

utans (*P. p. morio*) can be maintained in slightly logged forests. PloSOne 5, e11510.
doi:11510.11371/journal.pone.0011510.

- S16. Meijaard, E., Mengersen, K., Buchori, D., Nurcahyo, A., Ancrenaz, M., Wich, S., Atmoko, S.S.U., Tjiu, A., Prasetyo, D., Nardiyono, et al. (2011). Why don't we ask? A complementary method for assessing the status of great apes. PloS ONE 6, e18008.
- S17. Wich, S.A., Singleton, I., Nowak, M.G., Utami Atmoko, S.S., Nisam, G., Arif, S.M., Putra, R.H., Ardi, R., Fredriksson, G., Usher, G., et al. (2016). Land-cover changes predict steep declines for the Sumatran orangutan (*Pongo abelii*). Science Advances 2, e1500789. 10.1126/sciadv.1500789
- S18. Ancrenaz, M., Oram, F., Nardiyono, Silmi, M., Jopony, M.E.M., Voigt, M., Seaman, D.J.I., Sherman, J., Lackman, I., Traeholt, C., et al. (2021). Importance of orangutans in small fragments for maintaining metapopulation dynamics. Frontiers in Forests and Global Change 4, 560944. 10.3389/ffgc.2021.560944
- S19. Ministry of Environment and Forestry of Indonesia (MEF) (2010). Forest Zones Map. Jakarta, Indonesia.
- S20. Ministry of Environment and Forestry of Indonesia (MEF) (2018). Indicative Map of Community Forestry Area (PIAPS). Jakarta. Available at:
<http://webgis.dephut.go.id:8080/kemenhut/index.php/id/peta/petapiaps>.