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NATURE VS. HUMAN NATURE: THE SOCIO- ECOLOGICAL DIMENSIONS OF BIODIVERSITY CONSERVATION IN THE ANTHROPOCENE

Lin, Bing

Princeton, NJ : Princeton University

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NATURE VS. HUMAN NATURE: THE SOCIO-ECOLOGICAL DIMENSIONS OF BIODIVERSITY CONSERVATION IN THE ANTHROPOCENE

BING LIN

A DISSERTATION
PRESENTED TO THE FACULTY
OF PRINCETON UNIVERSITY
IN CANDIDACY FOR THE DEGREE
OF DOCTOR OF PHILOSOPHY

RECOMMENDED FOR ACCEPTANCE BY
THE PROGRAM IN SCIENCE, TECHNOLOGY, AND ENVIRONMENTAL POLICY IN
THE PRINCETON SCHOOL OF PUBLIC AND INTERNATIONAL AFFAIRS

ADVISER: DAVID S. WILCOVE

NOVEMBER 2024

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Abstract

My dissertation explores the socio-ecological dimensions of biodiversity conservation, situated at the intersection of conservation ecology, environmental policy, and behavioral science. Through five chapters, I examine the diverse impacts of human behavior on biodiversity and propose strategies to regulate unsustainable practices in ways that account for ecological, economic, and cultural trade-offs, as well as local contexts. Drawing from real-world conservation challenges, each chapter addresses the regulation of behavior at different scales—individual, collective, and institutional. In Chapter 2, I examine the risks that so-called wet markets pose to human health and biodiversity by creating a qualitative risk classification scheme for policymakers. I recommend targeted, risk-adjusted policies to better protect both human health and biodiversity without unnecessarily and unfairly hindering access to food for millions of people. In Chapter 3, I focus on the online ornamental marine fish trade in the United States. Sourcing e-commerce data from online aquarium retailers, I find a variety of marine fish to be sold, most of which are sourced exclusively from the wild, and many of which are of conservation concern. I call for improved transparency and sourcing methodologies to mitigate unsustainable trade. In Chapter 4, I use social media web-scraping and coral cover maps to explore the impact of coastal tourism on Hawaiian reefs. Higher live coral cover attracts reef visitors, but that visitation is correlated with subsequent reef degradation. Such feedback loops threaten the highest quality reefs, highlighting both their economic value and the need for effective conservation management. In Chapter 5, I focus on one form of on-reef visitation, scuba diving tourism, and address the regulatory reforms that are needed to mitigate diver-reef damages. Critiquing existing mitigation strategies, I propose comprehensive reforms to reduce diver impacts at various levels of legislative scale. In Chapter 6, I examine unsustainable tourist

behaviors on coral reefs in Southeast Asia using data from 730 divers and 20,419 minutes of observation. From both in-water observations and post-dive questionnaires, I find high levels of unintentional damage, with tourists systematically *overestimating* their diving abilities and *underestimating* their reef impacts, calling for adaptive management and stakeholder engagement.

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It takes a village to teach a boy to fish—or however the saying goes. The past five years, and the 25 before that, have been a wild ride, and one entirely on the coattails of a superhero cast of family, friends, colleagues, and mentors. The least I can do is properly cite my sources.

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To thriving ecosystems, empowered communities,
and sustainable coexistence for a world in crisis.

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Chapter 1 — Introduction

1.1: Context and Significance

The ongoing biodiversity crisis represents an unprecedented threat to both natural ecosystems and to humanity.[1,2] The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) estimates around one million species to face acute extinction risk within decades unless substantive changes are made to protect and restore nature.[3]

The biodiversity crisis not only threatens ecological integrity but also undermines the ecosystem services that are vital for human well-being, including food security, climate regulation, and disease mitigation.[4] Addressing this crisis requires urgent and coordinated global efforts to implement effective conservation strategies, sustainable resource management, and policies that promote biodiversity protection at all levels with as little friction as possible for stakeholder communites.[5]

The wildlife trade, encompassing both legal and illegal activities, is a particularly insidious driver of biodiversity loss that disproportionately threatens rare and endangered species with extinction.[6] According to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the illegal wildlife trade alone is estimated to be worth up to $20 billion annually, making it one of the largest black markets in the world.[7] Orthogonal to the markets' legality, the wildlife trade not only depletes wild populations, but also disrupts ecosystems and increases the likelihood of zoonotic disease outbreaks.[8]

Similar to the plight of terrestrial species, marine ecosystems are also under threat from various human activities. Coral reefs, in particular, are highly at risk. They are not only critical biodiversity hotspots that provide essential ecosystem services for hundreds of millions of

people worldwide, but they are also especially susceptible to small perturbations to ecosystem and abiotic conditions. Climate change, overexploitation, pollution, and habitat degradation are all anthropogenic stressors that directly threaten coral reefs and the quarter of all marine life that they sustain, as well as the numerous ecosystem services, such as fisheries, tourism, and coastal protection, that they provide.[9–12]

Using interdisciplinary methods implemented across scales and intervention types, my dissertation seeks to inform the socio-ecological dimensions of biodiversity conservation across several contexts. I first highlight critical threats to species conservation (and public health) in the context of both terrestrial and marine wildlife trade. These include the economic and ecological determinants of retail price as a market signal, emphasizing the need for targeted interventions that balance the needs of stakeholder communities and biodiversity conservation. I then explore the intricate inter-relationship between coral reefs and coastal tourists, underscoring the socio-ecological dynamics of reef degradation from coastal tourism and how best to mitigate these impacts.

A key focus of this research is on the complex trade-offs decisionmakers must navigate to balance conservation, development, and social equity. These trade-offs often manifest as double or even triple tensions between goals like preserving biodiversity, fostering economic growth, and ensuring equitable outcomes for communities dependent on natural resources.

Through case studies and multi-disciplinary analytical techniques, my research integrates ecological, economic, and social dimensions to propose adaptive management strategies and policy reforms. Ultimately, I aim to advance our understanding of how human

activities influence biodiversity and ecosystem health, offering actionable recommendations for conserving nature across various patterns of scale and intervention.

1.2: Interdisciplinary, Solutions-Based Approach

Unlike most disciplines, conservation science is crisis-driven, where the merits of the field are at least partly determined by the implications they might have for real-world conservation outcomes.[13] There is also a growing understanding of the formative role the behavioral sciences play in conservation research and practice.[14,15] Successes and solutions in conservation almost always necessitate some degree of individual or collective human behavior change, as most exigent environmental issues, such as climate change and biodiversity loss, are also the cumulative products of persistent human behaviors.[16] Thus, real-world conservation necessarily involves both understanding the extent of our human footprint on ecological systems and processes, as well as facilitating enduring yet equitable changes to human behaviors.

This research employs a diversity of qualitative and quantitative data collection methods, including social media–based web scraping, remote sensing, questionnaire survey instruments, behavioral observations, and open-source datasets. Such an interdisciplinary approach is critical for developing tailored regulations that address the socio-ecological complexities of conservation issues. Tailored regulatory mechanisms must be flexible to address the unique contexts of wildlife trade, coral reef conservation, and coastal tourism, while navigating the trade-offs involved in achieving conservation goals alongside economic development and social well-being.

Finally, my dissertation's headline title, *"Nature vs. Human Nature"*, also underscores the at-times contradictory goals of socio-economic growth and nature conservation. While my work operates within the framework of a human-centered perspective that values ecosystems primarily for the services they provide, this approach does not account for the importance of recognizing and preserving the inherent value of nature itself. There should be a holistic ethical lens through which humanity can recognize the inherent value of biodiversity, independent of the utility it confers to human societies. Until then, my research centers around pinpointing and implementing solutions that might reconcile these opposing interests in win-win scenarios—where both nature and human societies can thrive.

1.2: Research Outline

My dissertation addresses a series of interconnected research questions that span five chapters, each building on the other to explore the complexity of biodiversity conservation across various contexts. To begin, I investigate the socio-ecological conditions of the terrestrial and aquarium wildlife trade, focusing on the risks these activities can pose to species conservation and human health.

Chapter 2 starts with an in-depth exploration of wet markets—the trade of consumption-oriented, perishable goods in a non-supermarket setting. Wet markets are essential nodes in global food systems and especially prominent in the policy and research eye in light of their recent attention in the COVID-19 pandemic. Some wet markets have played a purported role in zoonoses, as well as in the legal and illegal wildlife trade, but by no means do all. To differentiate wet markets by their variable risks to human health and biodiversity, I propose a risk classification framework that identifies critical risk factors, including the

presence of high disease-risk animal taxa, hygiene conditions, market size, animal density, and the length of animal supply chains. By offering insights into the complexities of wet market dynamics, I advocate for targeted policies that effectively safeguard both human health and biodiversity, ensuring sustainable market practices without compromising food security.

Chapter 3 shifts focus to the online ornamental marine fish trade in the United States, a thriving industry shaped by consumer demand in the United States and facilitated primarily through e-commerce platforms. Employing comprehensive web-scraping techniques, I compile and analyze extensive data on species diversity, sourcing methods (wild-caught vs. captive-bred), economic dynamics, and their ecological ramifications. I show correlations between retail prices and sourcing methods, highlighting how market preferences can complicate conservation outcomes. This chapter specifically underscores concerns over unlisted species and the opacity of trade practices, calling for improved transparency and enhanced conservation efforts within the ornamental fish trade to mitigate impacts on marine biodiversity.

Together, the analysis of wet markets and the marine aquarium fish trade reveals the complexities inherent in wildlife trade and the need for nuanced policy interventions that can balance conservation with socio-economic considerations. These chapters collectively underscore the role of market drivers and consumer behavior in influencing conservation outcomes, setting the stage for tailored regulatory and behavioral solutions.

The subsequent chapters shift focus to the local, regional, and global level impacts of coastal tourism on coral reefs. In Chapter 4, I consider the co-dependence of coral reefs and coastal tourism across the Hawaiian archipelago. Drawing on Instagram-based social media

data and high-resolution coral cover maps, I examine how tourism activities can affect coral reef health and vice versa. I explore spatial and temporal patterns of tourism impacts, and reveal how visitor behaviors contribute to reef degradation through direct contact and indirect environmental pressures. By assessing the implications of coral health on tourist behavior and the ensuing feedback loops that threaten reef ecosystems, I also advocate for adaptive management strategies and emphasize the need for integrated management approaches that sustain ecosystem health while supporting local economies dependent on coastal tourism.

Chapter 5 addresses urgent regulatory reforms needed to mitigate coral reef damage caused by scuba diving tourism. I critique existing mitigation strategies and advocate for comprehensive reforms designed to reduce diver impacts on reefs. Through a review of successful policy interventions executed at various patterns of scale, I outline strategies to enhance reef protection and promote sustainable diving practices. I also underscore the importance of robust enforcement mechanisms and incentives to encourage compliance with regulations at various levels of implementation. Specifically, I investigate how policy interventions can shape social norms and behaviors among tourists engaging with coral reefs. I argue that a comprehensive understanding of the psychological and social determinants of unsustainable behaviors is critical, especially when such behaviors so clearly have long-term detrimental effects on reef health.

Lastly, in Chapter 6, I examine the underlying drivers of unsustainable tourist behaviors on tropical coral reefs in Southeast Asia. Using primary observational data and questionnaire survey instruments, I analyze tourist perceptions, behaviors, and their impacts on reef health. I identify key drivers of unsustainable practices, including misconceptions about

environmental impacts and the influence of tour operator practices. By integrating socio-ecological considerations, I propose proactive adaptive management strategies, stakeholder engagement, and the promotion of sustainable tourism practices that align with conservation goals and local community needs.

Through these investigations, I hope to not only addresses specific conservation challenges but also to offer a broader commentary on how human nature interacts with the natural world. The integrative focus on tailored regulation, coupled with an understanding of the trade-offs policymakers must consider, underscore the complexity of advancing conservation goals in a world where human interests and environmental health are inextricably linked. By weaving together these diverse topics, I emphasize the critical need for interdisciplinary approaches that consider the ethical, socio-economic, and ecological dimensions of conservation, while also proposing tangible solutions to the challenges that arise at the nexus of human activity and biodiversity preservation to conserve the ecosystems on which all life depend.

Chapter 2 — A better understanding of "wet markets" is key to safeguarding human health and biodiversity

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Abstract

"Wet markets" have been implicated in multiple zoonotic outbreaks, including COVID-19. They are also a conduit for legal and illegal trade in wildlife, which threatens thousands of species. Yet wet markets supply food to millions of people around the world, and differ drastically in their physical composition, the goods they sell, and the subsequent risks they pose. As such, policymakers need to know how to target their actions to efficiently safeguard human health and biodiversity without depriving people of ready access to food. Here, we propose a taxonomy of wet markets, oriented around the presence of live or dead animals, and whether those animals are domesticated or wild (either captive-reared or wild-caught). We assess the dimensions and levels of risk that different types of wet markets pose to people and to biodiversity. We identify six key risk factors of wet markets that can impact human health: presence of high disease-risk animal taxa, presence of live animals, hygiene conditions, market size, animal density/interspecies mixing, and the length/breadth of animal supply chains. We also identify key factors informing risk to biodiversity. Finally, we recommend targeted, risk-adjusted policies to more efficiently and humanely address the dangers posed by wet markets.

2.1: Wet market controversy

In the wake of the COVID-19 pandemic and its possible origin at the Huanan Seafood Wholesale Market in Wuhan, China, attention has focused on the threats that wet markets pose to both human health and biodiversity.[17,18] The pandemic triggered calls for the permanent closure of all wet markets in China and elsewhere.[19] Such calls came from policymakers,[20] heads of influential governmental organizations,[21] non-profit organizations,[22] public-health experts,[23] and even celebrities.[24]

A blanket condemnation of all wet markets presents at least three problems. First, imprecise language can foster xenophobia towards "foreign" cultures, especially with respect to long-standing and largely anodyne dietary practices.[25] Many wet markets sell only fresh produce and dead domesticated animals, and serve as the primary means of food acquisition and nutrition for a significant number of people in the world, especially in East and Southeast Asia.[26–30] When all types of wet markets are conflated and sensationalized as threats to human health,[31] anti-Asian sentiments can emerge.[32] Second, calls to ban all wet markets may be met by local or national resistance in countries where such markets abound, thereby blocking opportunities to target the types of wet markets that actually pose serious risks to people or biodiversity.[33] If sweeping bans on wet markets are nevertheless enforced, trade will likely be driven underground, making conditions even harder to quantify, regulate, and reform.[8] Finally, such censure also presupposes that markets themselves are the root cause of global pandemics. Instead, markets vary in risk, and represent just one node of zoonotic transmission potential in animals and along the global wildlife trade supply chain. Solutions that fail to differentiate between wet market types, or treat wet markets as the single modality from which pandemics might arise, ultimately miss the mark.[34]

In light of the impracticalities in closing all wet markets, calls for blanket wet market bans are being replaced by more targeted approaches. These include closing "high-risk" wildlife markets,[35] improving market biosecurity measures,[36] and calls to end the commercial trade of wild animals for consumption.[34] All these approaches would stand to benefit from a clearer classification of the different types of wet markets that exist, and the differential risks they pose. The Chinese government has responded with alacrity to the COVID-19 crisis by banning the commercial sale and consumption of most terrestrial wildlife in China.[37] However, precedents of policy rollbacks,[38] deep-rooted cultural predilections favoring the consumption of wild animals,[39,40] and abiding zoonotic risks from domesticated animals, point to the value of having a way to rank the relative risks to human health and biodiversity of different types of wet markets, both in China and in countries without widescale wildlife-consumption bans in effect. Here, we propose a typology of wet markets to better delineate risks in existing market structures, and we provide a qualitative risk assessment for use by policymakers.

2.2: What are wet markets?

The term "wet market" has been used for decades to describe a broad class of markets that has existed for centuries. They were originally named after their frequently wet floors, a result of regular washing to keep stalls clean, plus the melting of the ice used to keep foods fresh.[41] In countries in East and Southeast Asia, like China, Taiwan, Thailand, Indonesia, Vietnam, Singapore, and the Philippines, wet markets often comprise rows of individual vendor stalls offering consumption-oriented, perishable goods (i.e., fresh meats and produce), in an open- or partially open-air setting.[42]

Thus, the term "wet market" can denote markets ranging from those selling just fruits and vegetables, to those selling exotic or endangered wildlife for consumption. For effective policy formulation, it is essential to recognize critical distinctions among these types of markets, as their associated risks also differ. *Wet markets* sell consumption-oriented, perishable goods in a non-supermarket setting. *Wildlife markets* sell non-domesticated wild animals, alive or dead, captive-bred or wild-caught. *Live-animal markets* sell live animals. Accordingly, some wildlife and live-animal markets are indeed wet markets, while others are not (Figure 2.1). The Huanan Seafood Wholesale Market in Wuhan, China, for instance, was a wildlife market, a live-animal market, and a wet market, selling an array of live and dead domesticated animals alongside non-domesticated species like bamboo rats (*Rhizomys sinensis*), palm civets (*Paguma larvata*), badgers (family *Mustelidae*), and wolf cubs (*Canis lupus*) for consumption.[43] Conversely, the Barito, Jatinegara, and Pramuka bird markets in Jakarta, Indonesia, are live-animal and wildlife markets but not wet markets; they sell live birds and other animals for use as pets, but not as food.[44] Similarly, the famous Dried Seafood Market on Des Voeux Road West in Hong Kong sells foods and medicines, but virtually all of its items are non-perishable, thereby excluding it as a wet market (Figure 2.2).[45]

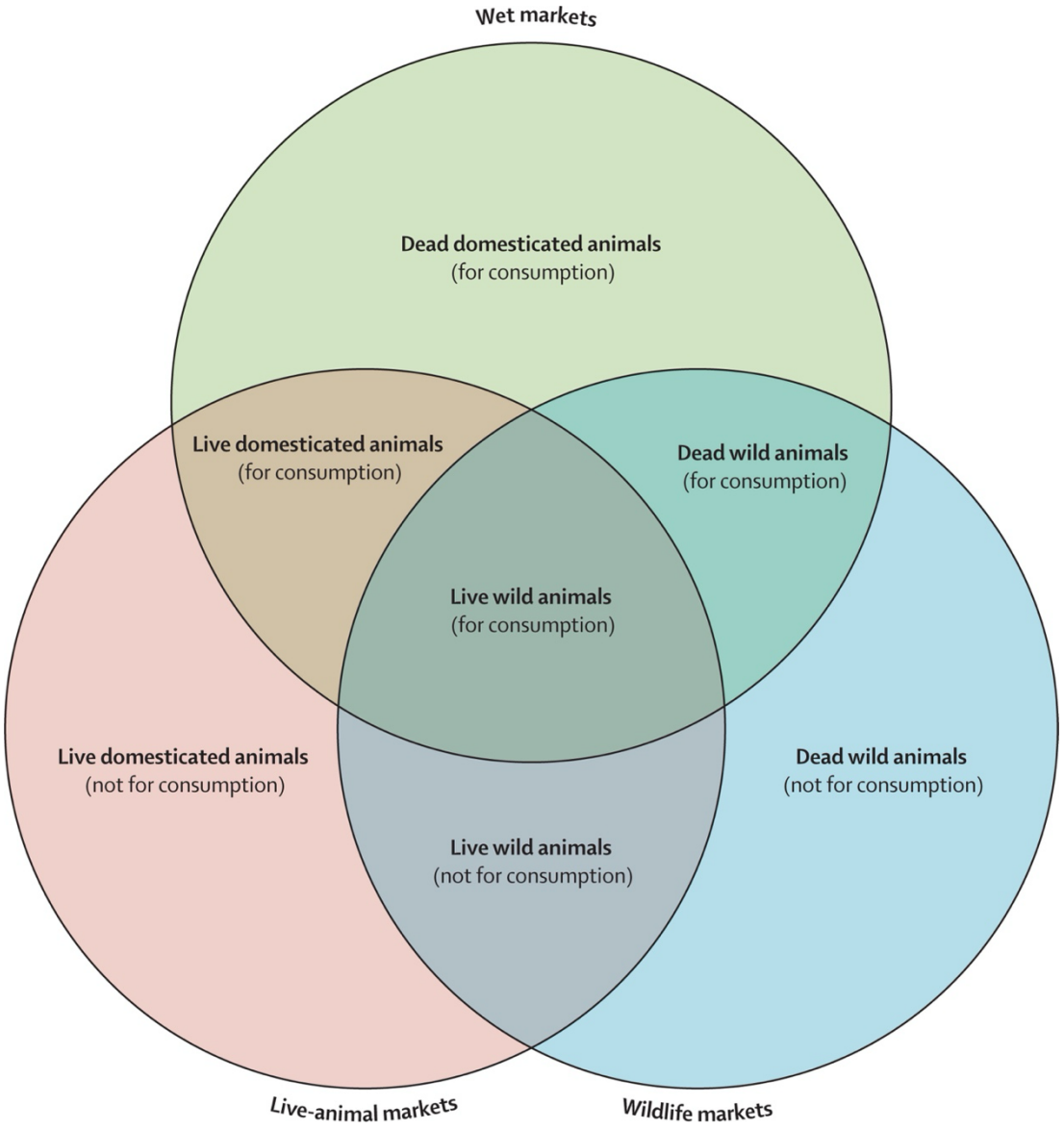

Figure 2.1: *Wet markets, live-animal markets, and wildlife markets. Markets are separated on three dimensions based on the condition, type, and intended usage of its animals: alive versus dead, domesticated versus wild, and consumption-oriented versus not consumption-oriented.*

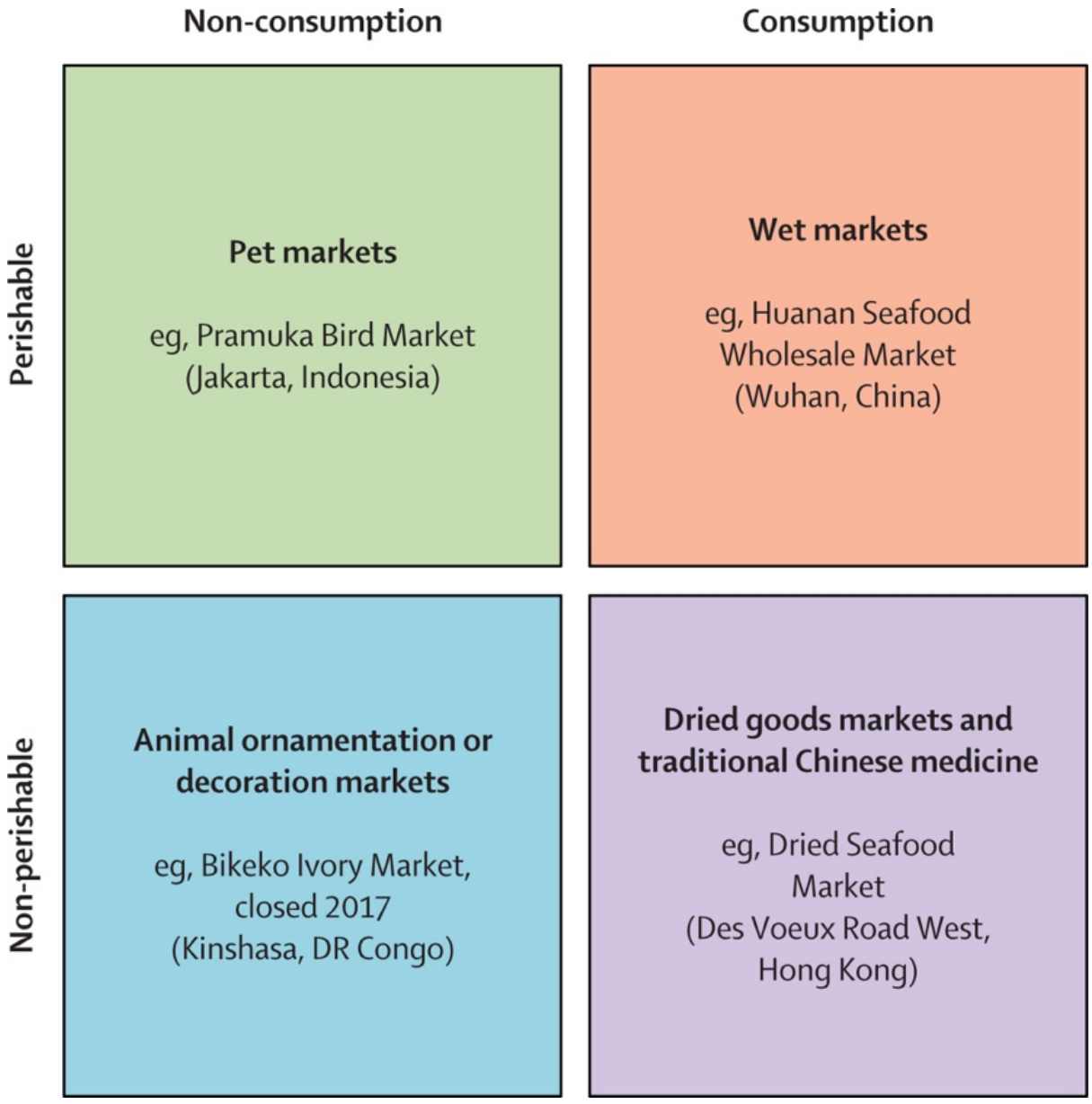

Figure 2.2: *Animal markets classified according to the types of goods sold. Wet markets sell consumption-oriented, perishable goods, whereas other types of markets sell animals and animal products in other forms, oriented for other purposes.*

2.3: Wet market risks

Risk encompasses both the likelihood of an undesirable event occurring and the repercussive severity of such an event were it to occur. Humans may have higher exposure to pathogens in domesticated animals, for example, which can result in repeated zoonotic infections.[46] On the other hand, people may have lower exposure to pathogens in wild animals, yet that exposure can nonetheless trigger major disease outbreaks (e.g., SARS, Ebola, monkeypox, Nipah virus, and COVID-19, all of which likely trace their provenance to markets, farms, or pet stores selling wild animals). This makes risk important but difficult to quantify and compare within categories of wet markets. Different risks can interact with one another, but assuming they compound cumulatively (though not necessarily linearly), we can rank markets according to their aggregate risks and identify those deserving of more immediate attention from health or conservation officials. In this paper, we focus on the risks of wet markets to human health and biodiversity loss, as these are well-represented by specific market characteristics, and are both increasingly exigent and important to address in light of possible future pandemics and the magnitude of the wildlife trade.[6]

2.4: Risks to human health

Many factors elevate a wet market's risk potential to human health. Here we focus primarily on factors associated with emerging infectious diseases (EIDs), due to the scale and cost of such events.[47,48] In general, the building blocks of EID outbreaks consist of interspecific zoonotic transmission, viral amplification, and viral modification.[49,50] Below we identify six key characteristics of wet markets that can induce or facilitate such risks: high disease-risk taxa,

live animals, hygiene, market size, animal density/interspecies mixing, and supply-chain length/breadth.

2.4.1: High disease-risk taxa

Certain taxa sold at wet markets may pose a greater risk to human health than others. A species' phylogenetic relatedness to humans plays an important role in determining its potential for zoonotic spillover. In general, the more phylogenetically related a species is to humans, the more likely that diseases affecting that species can adapt to human hosts.[51] Empirically, this may be why most EIDs in humans have a mammalian origin.[52]

A species' disease risk to humans may also be correlated with the richness of that species' taxonomic order, its global abundance, and its inherent likelihood of harboring zoonotic pathogens.[53–55] Taken together, rodents (order Rodentia), bats (Chiroptera), primates, carnivores (Carnivora), and ungulates (primarily Artiodactyla) may all exhibit elevated zoonotic potential within mammals. With the exception of some ungulate species, most of the individuals from these orders found in wet markets are from non-domesticated species, some of which are wild-caught, others of which are captive-bred. Recently, the utility of using intrinsic species-specific characteristics to predict zoonotic risk has been challenged, suggesting that a focus on canonically "high disease-risk" species in wet markets and elsewhere may not be as useful as once believed.[56] Pending further research that confirms or refutes this challenge, we continue to recognize some taxonomic groups as being of higher disease-risk than others.

Irrespective of a host-neutral outlook on zoonotic risk, since wildlife pathogens have caused over 70% of zoonotic EID events and virtually all pandemics in recent years,[47] exposure

to species not commonly in contact with humans likely elevates the potential severity of disease risks.[56,57] This is not to say that zoonoses from domesticated animals should be overlooked, as they can be deadly.[46,52] Rather, as human populations come increasingly into contact with previously isolated populations of wildlife, a complex interplay of viral adaptation between wild species, domesticated species, and people, can facilitate the emergence of novel zoonotic diseases,[57,58] and through increased virulence, rapid spreading, and lack of existing medical knowledge or treatment, these can be uniquely harmful to humans.[59,60]

We note that many publications highlighting the risks to human health from "wildlife" do not specify whether they are referring to wild-caught animals or captive-bred individuals of non-domesticated species (e.g., farmed civets).[47,53,61] The degree to which wild-caught animals may pose a greater risk to human health from EIDs than do captive-bred, non-domesticated animals remains uncertain and deserves additional research attention (we return to this distinction in our discussion of wet market risks to biodiversity).

2.4.2: Live animals

The presence of live animals in wet markets poses elevated risks of viral pathogen transmission. The inter- and intra-species mixing of live animals can facilitate pathogen shedding and viral recombinations in new hosts, which in turn may heighten the pathogenicity of animals to each other and to humans.[62] Heightened stress levels of captive animals (i.e., high densities in confinement, new environments, unfamiliar interspecies contact, etc.) can further compromise immune system responses and increase zoonotic disease transmission and virulence.[63,64] Exposure to live poultry in the marketplace, for instance, was a significant risk

factor in the viral spread of avian influenza during the 1997 H5N1 outbreak in Hong Kong.[65] This is an even greater concern in markets harboring wild animal species, which often exhibit greater stress responses to transport or market conditions than do domesticated animals.[66]

2.4.3: Hygiene

Lack of hygiene is a significant risk factor for human health in wet markets, both through limited or unenforced biosecurity controls in markets themselves, and through hygiene risks magnified along lengthy supply chains of live animals. In wet markets without live animals, lapses in hygienic practices have been linked to bacterial and parasitic infections, often through the improper handling or storage of carcasses, polluted water, or proximity to other contaminants.[62,67] In wet markets with live animals, there is the additional risk of viral zoonoses, which can lead to EID outbreaks.[68,69] To mitigate risks, vendor handwashing, routine cleaning practices, and separation of different species can have positive health outcomes, while improper waste disposal and inadequate sanitation measures can exacerbate negative health outcomes.[70]

2.4:4: Market size

Market size can be defined in several ways (e.g., trade volume, market spatial extent, number of customers or transactions, etc.), but is generally related to the total number of people present and goods sold. As food handlers and market-goers are often primary patients of zoonotic diseases, larger markets servicing larger numbers of people pose greater human health risks than markets serving fewer people, given a constant density of vendor stalls and people. This is because larger markets increase the initial pool of susceptible hosts, along with their total exposure to pathogens, from both animals and from each other.[62] In the SARS epidemic of 2003, around 40% of early patients were food handlers with probable animal

contact; most of these patients lived closer to wet markets than to animal farms, suggesting that markets, not farms, were the initial source of transmission.[71] Animal handlers in these markets also had a significantly higher prevalence of SARS-CoV antibodies than vegetable sellers in the same markets, corroborating this assertion.[72]

2.4.5: Animal density and interspecies mixing

The density of animal species within wet markets and along animal supply chains is important for viral disease transmission. Depending on a market's layout and the proximity of animals to each other, high animal densities can facilitate transmission of disease within animal species, between species, and between animals and humans.[73–75] Higher animal densities increase the likelihood of interspecies mixing and subsequent cross-contamination, which can lead to viral spillover, adaptation, and subsequent zoonotic disease emergence.[76–78] Such conditions, facilitated by a dearth of marketplace hygiene, was the hypothesized reason for the viral spillover of SARS from horseshoe bats (*Rhinolophus* sp.) to civets (*P. lavarta*) in 2003.[79]

2.4.6: Supply chain length and breadth

Because transport to end consumers includes the close confinement of live animals, often under unhygienic conditions, lengthy supply chains can increase pathogen transmission and amplify disease risks. In a study of wild field rats (*Rattus* sp. and *Bandicota* sp.) in Vietnam, coronavirus presence was shown to magnify along the supply chain, culminating in the highest levels at markets and restaurants.[80] Just as lengthy supply chains prolong the interspecies mixing of live, stressed animals, the multi-origin sourcing of animals also elevates the potential for novel viral combinations.[70,81] This is especially relevant when wild species are introduced in unusual groupings with other wild or domesticated species, thereby facilitating unnatural viral spillovers.

2.5: Risks to biodiversity

The wildlife trade is a significant global driver of biodiversity loss, and affects one in every five vertebrate species, including many that are endangered.[6] In wet markets, the criteria for assessing biodiversity risks focuses on which animal species are being sold, rather than on how such species are sold or on market conditions. Considered simply, wet markets that pose the greatest risk to biodiversity are those that serve as a conduit for the (often illegal) sale of threatened or declining wild species.

Threatened species are those with elevated extinction risks, according to their IUCN Red List status ("Critically Endangered", "Endangered", and "Vulnerable"),[82] some of which have been found for sale in wet markets [e.g., the Sulawesi fruit bat (*Acerodon celebensis*) in Indonesia, listed as "Vulnerable" on the IUCN Red List;[83] the Bengal slow loris (*Nycticebus bengalensis*) in Lao PDR, listed as "Endangered" on the Red List;[68] and the Sunda pangolin (*Manis javanica*) in Myanmar, listed as "Critically Endangered" on the Red List].[84] Declining species include those that are not currently threatened (according to the Red List), but whose populations are declining rapidly enough to suggest they are approaching imperilment. These species can be recognized by other signals, such as population trend data provided by the IUCN Red List, increasing prices and declining sales volumes in markets,[85] their placement on national or sub-national (i.e., state or provincial) threatened-species lists, CITES seizure data, or as designated by various scientific authorities. BirdLife International, for example, estimates that at least 40% of the world's bird species are declining.[86]

Overall, the sale of domesticated animal species in wet markets poses little *direct* risk to biodiversity, but this is not the case for the sale of many wild species, either captive-reared or wild-caught. The distinction between wild-caught animals and captive-bred, non-domesticated

animals is relevant here. Domestication is essentially a sustained, multi-generational, mutualistic relationship between animals and humans, characterized by intentionality on the part of humans in the selection of particular traits in the species being domesticated.[87] This implies both a cultural and biological component to domestication, which complicates any simple binary classification. Each and every species cannot be tagged as either fully domesticated or fully wild. As such, we encourage recognition of three groupings of species: domesticated species that have undergone many generations of human-controlled reproduction (e.g., poultry and cattle), non-domesticated but commonly captive-reared species (e.g., farmed porcupines, pythons, and bamboo rats), and wild-caught species (e.g., certain species of bats, monkeys, and pangolins).

The sale of wild-caught individuals of threatened or declining species presents a clear threat to biodiversity, as it directly contributes to species' extinction risk. Alternatively, the commercial farming of wild species (as distinct from the captive-breeding of threatened species solely for conservation purposes)[39,88] is sometimes presented as a way to sustainably produce threatened species for consumption.[89] However, biosecurity concerns, economic barriers to entry, and cultural predilections favoring wild-caught meat mean that wildlife farms have yet to replace other forms of wildlife acquisition (e.g., hunting or poaching) in many markets.[90,91] Additionally, because wildlife farms may require periodic restocking from wild-caught specimens, their efficacy in aiding conservation efforts remains uncertain.[91,92] As such, the sale of threatened or declining species in wet markets, regardless of origin, should be grounds for biodiversity concern.

There is a relatively small number of species that are imperiled in the wild but abundant in captivity. For example, the American bison (*Bison bison*) is classified by the IUCN Red List as "Near-Threatened",[93] despite also being raised commercially for its meat. Unless the commercial farming of such species facilitates laundering of illegally harvested individuals from wild populations,[94] the presence of such species in wet markets is not evidence of a risk to biodiversity.

Finally, it should be noted that risks to biodiversity are further elevated, indirectly, by habitat destruction and infrastructure that facilitates access to novel species. Habitat destruction imperils sensitive species that are not themselves directly extracted for sale and consumption.[95] Improved access to wildlife habitats also increases trade volumes of captured animals, and magnifies risks to human health.[96,97] It is also clear that demand for domesticated-animal products, in wet markets and elsewhere, helps to sustain the expanding livestock industry, a major driver of habitat loss.[98,99] While such secondary risks are important, they pertain to the entire livestock industry and meat consumption as a whole, and so are excluded from consideration here.

2.6: A risk framework across wet market types

By creating a taxonomy of different wet market types and classifying their relative risks to human health and biodiversity, we can better articulate where public health and conservation efforts should be directed most urgently. Though wet markets differ from market to market and instance to instance, we identify a progression of four broad wet market types:

1. Markets selling *no live animals* (excluding seafood) for consumption and only domesticated-animal products, alongside anything else (e.g., fruits and vegetables).

2. Markets selling *live domesticated animals* for consumption, alongside anything else (possibly including dead domesticated-animal products).

3. Markets selling *dead wild animals* (either captive-reared or wild-caught) for consumption, alongside anything else (possibly including live domesticated animals, and dead domesticated-animal products).

4. Markets selling *live wild animals* (either captive-reared or wild-caught) for consumption, alongside anything else (possibly including dead wild animals, live domesticated animals, and dead domesticated-animal products).

In addition to outlining the risks these wet market types pose to EIDs and biodiversity, we also qualitatively assign risk levels (low, medium, and high) from the seven identified health and biodiversity factors to each market type (Table 2.1). As risk designations are subjective and interactive with other factors, this framework informs cumulative risks to human health and biodiversity of different wet market types, but does not enumerate individual risks viewed in isolation of other factors.

2.6.1: Wet markets with no live animals

This category likely constitutes most wet markets, and certainly constitutes the direction many wet markets in Asia are heading.[41,100–103] Relative to other market types, wet markets selling no live animals (and only dead domesticated-animal products) present the lowest risks to both human health and biodiversity. They pose no direct threat to biodiversity loss (though consequential biodiversity concerns associated with meat consumption remain), as they contain no wild animals, and they have not been associated with the presence or

propagation of any historical EID events. However, such markets are often informal and unregulated, thereby still presenting parasitic and bacterial foodborne health risks largely driven by inadequate hygiene practices.[67]

After banning the sale of live poultry in the 1990s and 2008, wet markets in Singapore and Taiwan, respectively, now all fall under this category (this excludes live seafood, which has historically had lower associated zoonotic risks relative to other types of animals).[41,100,104] As of July 2020, China has also announced its plan to phase out all live poultry from its wet markets in response to the COVID-19 pandemic,[102] supplementing its earlier nationwide ban on the use of wildlife for food consumption (though not for medicine) in February 2020.[103]

2.6.2: Wet markets with live domesticated animals

In this market type, live domesticated animals are present and slaughtered on customer demand. Such animals often consist of just poultry and seafood (e.g., some wet markets in Hong Kong),[105] but other live domesticated animals can also be present. While such markets present no direct threat to biodiversity, the presence of live (domesticated) animals escalates the human health repercussions of increased animal densities, interspecies mixing, long supply chains, multi-origin sourcing, and a lack of hygiene.[81] This elevates health risks to animal handlers and market-goers at all points along the supply chain, as live animals are better channels for pathogen shedding and viral amplification than dead animals.[65,72,106] Short of permanently closing all such live-animal wet markets, periodic but temporary market closures for cleaning and disinfecting can decrease viral presence.[107,108]

2.6.4: Wet markets with dead wild animals

Such markets sell dead wild animals, either wild-caught or captive-bred, but may also include live or dead domesticated animals for sale. This and subsequent categories of wildlife wet markets are much rarer than wet markets selling just domesticated animals,[101] but the Tomohon Extreme Market in Sulawesi, Indonesia is one such market, selling dead wild animals like fruit bats (*Acerodon celebensis* and *Pteropus alecto*), snakes (*Python* sp.), and wild pigs (*Sus celebensis*), alongside live and dead domesticated animals like chickens, ducks, and dogs (as of February 2019).[83] In addition to the risks posed by live domesticated animals in wet markets, the presence of dead wild animals presents additional health risks through the inclusion of more high disease-risk taxa, which increases the likelihood of novel pathogens and interspecific spillover, including to humans, along the supply chain. Importantly, such markets also present meaningful risks to biodiversity when threatened or declining wild species are sold. The Tomohon Extreme Market, for instance, has been known to source the Critically Endangered Celebes crested macaque (*Macaca nigra*), a banned but favored delicacy of the local Minahasan community in Sulawesi.[83]

2.6.5: Wet markets with live wild animals

Such markets include the purported source of the SARS-CoV-2 outbreak, the Huanan Seafood Wholesale Market in Wuhan, China, which sold live and dead wildlife like bamboo rats (*R. sinensis*) and badgers (Mustelidae) alongside live and dead domesticated animals.[43] Live animals facilitate zoonotic transmission; wild animals often comprise high disease-risk taxa with potential for novel EIDs; and live and wild animals together pose the greatest

cumulative threat to human health of any wet market type. Even with proper hygiene and market practices, such markets' inherent risks to human health are difficult to mitigate. They also present unavoidable risks to biodiversity when the wild species sold are threatened or in decline.

	Wet market types			
	(1)	(2)	(3)	(4)
	Dead domesticated animals, excluding live seafood	**Live domesticated animals**, including any of **(1)**	**Dead wild animals**, including any of **(1)** or **(2)**	**Live wild animals**, including any of **(1)**, **(2)**, or **(3)**
High disease-risk taxa present	**Low** No historical EID events have been linked to such markets	**Medium** Live domesticated animals in wet markets have been linked to past EID outbreaks such as avian influenza[48]	**High** Wild animals in wet markets can comprise high disease-risk taxa for EIDs[33]	**High** Same as (3)
Live animals present	**NA** No live animals sold in such markets	**Medium** Live animals facilitate viral shedding and zoonotic transmission;[48,63] stress increases live animals' susceptibility to infection[49,50]	**Medium** Same as (2)	**High** All of (2), and live wild animals can display greater stress responses to transport or market conditions than domesticated animals[52]
Poor hygiene	**Low** Poor hygiene elevates the risk of foodborne illnesses[53,55]	**High** Poor hygiene elevates the risk of zoonotic EID events[48]	**High** Same as (2)	**High** All of (2), and the presence of live, wild animals elevates the risk of EID events[48,54]
Large market size	**Low** No historical EID events have been linked to such markets	**Medium** Larger markets increase the pool of susceptible human and animal hosts to EID spillovers[51,57,58]	**High** All of (2), and wild and domesticated animals sold together elevates the risk of EID events[48]	**High** All of (3), and the presence of live, wild animals elevates the risk of EID events[33]
High animal density and interspecies mixing	**Medium** The tight confinement of live, domesticated animals along the supply chain can pose health risks[63]	**High** Interspecies contact facilitates viral spillover and amplification along the supply chain and at markets[61,63,85]	**High** All of (2), and the presence of high disease-risk taxa elevates the risk of EID events along the supply chain[33,86]	**High** All of (3), and the presence of high disease-risk taxa elevates the risk of EID events at markets
Long length and breadth of supply chain	**Medium** Lengthy supply chains can exacerbate hygiene issues and interspecies mixing;[66] multiorigin sourcing can facilitate viral spillover[56]	**Medium** Same as (1)	**High** All of (1), and wildlife supply chains can be lengthier or more irregular than those of domesticated animals and elevate the risk of EID events[66]	**High** Same as (3)
Threatened or declining species sold	**NA** No threatened or declining animal species sold in such markets	**NA** No threatened or declining animal species sold in such markets	**High** Wild animals in wet markets can be of threatened or declining species (see section entitled Risks to biodiversity)[54]	**High** Same as (3)

Table 2.1: Taxonomy of EID and biodiversity risk across wet market types. EID=emerging infectious disease. NA=not applicable.

2.7: Looking forward

Wet markets come in many shapes and sizes, are widespread throughout the world, and serve essential needs of numerous people. Some wet markets pose a significant threat to human health and biodiversity, but by no means do all. Hence, a broad-brush treatment of wet markets to address concerns about EIDs and/or biodiversity loss lacks context, and is likely to face significant resistance from both vendors and customers. A targeted approach may prove more effective, starting with a qualitative risk analysis that recognizes the variety of wet markets.

To assess risks to human health, we identify six key aspects of wet markets: (1) the presence of higher disease-risk taxa, (2) the presence of live animals, (3) hygiene conditions, (4) market size, (5) animal density/interspecies mixing, and (6) supply chain length/breadth. To determine risks to biodiversity, we identify threatened species by their extinction risk in the wild (represented by their IUCN Red List status), and declining species by metrics such as IUCN Red List population trend data, threatened-species lists, and changes in market prices and availability. These criteria are not exhaustive, but they allow us to begin to build a risk framework to identify which types of wet markets cumulatively engender the greatest threats to people and biodiversity. Future research can bolster this with quantifiable ways to assess, isolate, and compare risks across market types and risk dimensions.

The cumulative risks of different wet markets to both human health and biodiversity appear inversely proportional to their prevalence and popularity.[101] Most wet markets likely pose comparatively little risk to human health or biodiversity, but a few pose a disproportionately large risk. When classified based on the presence or absence of live and wild animals, wet markets can be arranged along a nested progression of risks to human health and

biodiversity, culminating in the proportionately small number of wet markets selling live, wild animals that have been the source of many previous EID outbreaks.

Looking forward, policymakers should prioritize regulating these markets and taking steps to prevent a resurgence of their most at-risk aspects (e.g., bans on the trade of wild-caught vertebrates for consumption), before turning their attention to other types of wet markets that pose less risk to people or biodiversity. Doing so will minimize harmful disruptions to communities, while diminishing market-associated risks to health and biodiversity. If only in the narrow context of human health, channeling scarce national and international resources towards targeted reductions in zoonotic risk in wet markets and elsewhere can help circumvent the next global pandemic. In the context of biodiversity, targeting those markets that sell threatened or declining species, either alive or dead, can close a consequential outlet for unsustainable and often illegal wildlife trade. In the context of human, animal, and planetary well-being, realistic and effectively targeted reform is preferable to sweeping but ineffectual change.

Search Strategy and Selection Criteria

This Personal View draws from our reading of the medical and conservation peer-reviewed literature in English, from July to December 2020. Search terms used to find peer-reviewed articles in Google Scholar included a combination of: “wet market”, “wildlife”, “zoonosis”, “emerging infectious disease”, and “wildlife trade”. Contemporary news articles, drawn from both English and Chinese sources, were used to contextualize the public controversy surrounding wet markets. The studies cited are not exhaustive but were chosen in

relation to their pertinence to wet markets, human health, or biodiversity, with a particular geographic focus towards East and Southeast Asia.

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Chapter 3 — The online ornamental marine fish trade in the United States

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Abstract

The global ornamental marine fish trade is a multi-billion-dollar industry, largely driven by demand from the United States. Much of this trade occurs online. We web-scraped four of the largest online e-commerce platforms selling ornamental marine fish in the United States, collecting data on fish taxa, prices, and sourcing methodology (wild-caught vs. captive-bred), which we supplemented with additional economic and ecological traits from Fishbase and the IUCN. We report 660 unique fish species sold, 88.9% (587 species) of which were sourced exclusively from the wild. Thirty-nine fish species were of conservation concern (threatened species or species with decreasing population trends according to the IUCN), with 32 of these species sourced solely from the wild. Retail prices were significantly correlated with source (captive-bred vs. wild-caught), body length, minimum occupied depth, and schooling behaviors. One hundred fifty-three species sold were not listed as being traded in either Fishbase or IUCN, indicating a dearth of information on this lucrative market. For the 58 species that were available as both wild-caught or captive-bred, captive breeding significantly reduced prices (mean 36.7% ± 20.9% SD reduction in price), underscoring its potential to meet rising demands for ornamental fish without drawing from wild populations.

3.1: Introduction

The trade in ornamental marine fishes is a lucrative industry that continues to expand globally. Encompassing a network of over a hundred countries, the trade involves well over a thousand marine fish species, many of which are extracted from their natural habitats to meet growing international demand.[109–111] Despite its substantial economic size and reach, as well as its increasing size, especially in the United States, the ornamental marine fish trade has received less scientific and regulatory scrutiny than other wildlife markets.[6,112,113] This lack of information and oversight obfuscates the trade's true scale and extent, posing major challenges to both assessments of its ecological impacts and efforts to implement and monitor controls.[112,114–118]

The vast majority of species involved in the ornamental marine fish trade are sourced from wild populations, which raises potential concerns for species overexploitation.[111] This exacerbates other threats to wild populations and increases the risk of extinction for those species already classified as threatened or facing population declines. Moreover, target species often experience elevated mortality rates throughout the process of capture, holding, transportation, and sale.[109] Capturing wild fish for the trade can also impact non-target species through incidental mortality and cause ecosystem changes stemming from the removal of functionally important species.[119] Beyond these immediate threats, the marine aquarium trade can also facilitate the accidental introduction of non-native species across biogeographical boundaries. These introductions can result in species-, population-, and ecosystem-level impacts, with additional downstream consequences for the economies where invasive species are introduced.[112,114,120] Such consequences underscore the urgent need for better data on the

nature of the trade and when regulatory measures and proactive conservation strategies are needed to mitigate the trade's deleterious effects on marine biodiversity and ecosystem integrity.

The United States stands out as a major hub in the ornamental marine fish trade. It consistently sits atop global importation charts, and plays a pivotal role in shaping global market trends.[110,112] Much of this growth has come from the recent convenience and accessibility offered by e-commerce platforms, which began dominating sales in the 2000s,[121] and now constitutes a primary way through which hobbyists can source aquarium fish within the USA. These factors, coupled with the largely opaque nature and structure of online markets, point to the outsized yet underexamined role of e-commerce platforms in the trade of marine fishes.

Here, we aim to provide an assessment of the online ornamental marine fish trade in the United States by surveying four of its largest online retailers of marine fish. Specifically, we collected data on: (1) the types of fish traded across these e-commerce platforms; (2) the per-unit price of each fish species (or phenotype) sold; and (3) where these fish populations were sourced (i.e. wild-caught vs. captive-bred, hereafter referred to as "fish source"). For each species sold, we also gathered additional ecological and economic trait data from Fishbase and the International Union for Conservation of Nature (IUCN) to generate an assessment of the primary drivers of price. We evaluated the extent to which the online trade is tied to the wild capture of fish and assessed the need of either captive breeding programs or sustainable fisheries to serve as commercially viable alternatives to unregulated wild capture amidst growing conservation concerns.

3.2: Methods

To assess the state, scale, and scope of the online marine aquarium fish trade, we conducted an analysis of four of the largest saltwater fish dealers in the United States: Live Aquaria, Blue Zoo Aquatics, Saltwaterfish.com, and That Pet Place (see Appendix for inclusion criteria and inter-dealer species accumulation curve). From July 2021 to August 2022, we collected information on the taxonomic identity, dealer-reported fish source (captive-bred or wild-caught), geographic region (if wild caught), and retail price (mean price for multiple listings) for each marine fish specimen (species or phenotype) sold on each of these online e-commerce platforms. Search results were filtered to include only marine ray-finned fish (*Actinopterygii*), and only those families that had at least 30 unique species for sale or that contained any number of captive-bred species. Since wild-caught species predominated in our dataset, this approach provides a biased but conservative estimate of the true ratio of aquacultured to wild-derived fish available for sale. Other fish taxa (e.g., sharks and rays, *Chondrichthyes*) and non-fish reef species, including invertebrates (e.g., stony corals, *Scleractinia*), were excluded from consideration (see Appendix for details).

For each recorded species, we extracted additional economic and ecological trait information from Fishbase and IUCN, including each species' maximum body length, occupied depth range, commercial and aquarium usage, diet, schooling behavior, and additional life history traits (see Appendix for full list of traits). We also obtained each species' extinction risk status and population trend data (e.g., "Stable" or "Decreasing") from the IUCN Red List. (While extinction risk exists on a spectrum, we consider species classified by IUCN as

Vulnerable, Endangered, and Critically Endangered by the IUCN as "threatened" in this study.)

To assess price correlates, we used a linear mixed effects model and Akaike information criteria corrected for small sample sizes (AICc) for model selection. Both family and IUCN threat status were treated as random effects, and we evaluated the relative contributions (fixed effects) of each species' maximum length, dietary preferences, schooling behavior, geography, minimum occupied ocean depth, occupied depth range, and fish source in an information theoretic framework (see Table A3.1 for model list). We utilized a paired t-test for matched price comparisons between species that had both wild-caught and captive-bred specimens available for sale. All analyses were conducted in R version 4.3.2, with the "nlme" and "MuMIn" packages used to conduct the linear mixed effects modelling and AICc evaluations, respectively.

3.3: Results

We identified 660 fish species (and 781 unique phenotypes) that were traded across all four e-commerce platforms (in order to derive mean inter-platform retail prices). The distribution of traded species spanned 12 families; wrasses (*Labridae*) had the largest number of species available for sale, followed by damselfishes/clownfishes (*Pomacentridae*), and gobies (*Gobiidae*) (Figure 3.1). 88.9% (587 of 660) of these species were sourced solely from the wild, 8.8% (58 of 660) of species were sourced both from the wild and through captive breeding, and 3.8% (25 of 660) of species were sourced exclusively through captive breeding programs.

Across all species sold, 4 species were listed as Endangered by the IUCN Red List, 16 species were listed as Vulnerable, and 27 species had Decreasing population trends. Of the 20

threatened species, 14 species were sourced exclusively from the wild. An additional 32 species were classified as Data Deficient, 24 were Not Evaluated, and 458 species had Unknown or unavailable population trends. Further, 153 species were not listed as being part of the aquarium trade on either the IUCN Red List or Fishbase despite their presence on the e-commerce platforms.

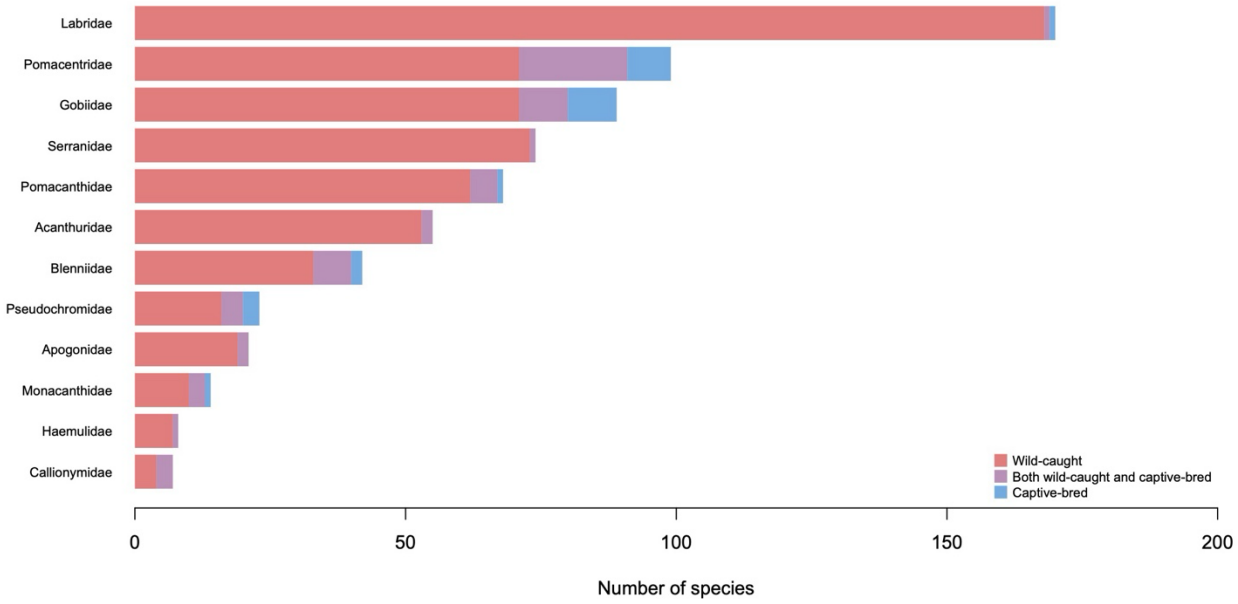

Figure 3.1: *The number of fish species by taxonomic family involved in the online ornamental fish trade in the United States, differentiated by source.*

The mean price of a specimen across all four e-commerce websites was 174.5 ± 50.8 USD (mean ± 95% confidence interval) (Figure 3.2). The median price was 64.5 USD, and the 25% and 75% quantile prices were 37.9 USD and 120.1 USD, respectively (Figure 3.2). We also found prices to vary by both IUCN threat status and taxonomic family (see Figure 3.2 and Table A3.2 for summary statistics).

We found retail prices to be significantly associated with fish source (captive-bred vs. wild-caught), maximum length, minimum occupied depth, and schooling behavior. This was indicated by the best performing model (ΔAICc = 0) from a 17-candidate model list (see Table A3.1 for model performance evaluations). The next best performing model included dietary preference as an additional fixed effect (ΔAICc = 2.0). On average and across all species, specimens that were wild caught, smaller in size, found in shallower waters, and that exhibited schooling behaviors were associated with lower prices (Figure 3.3).

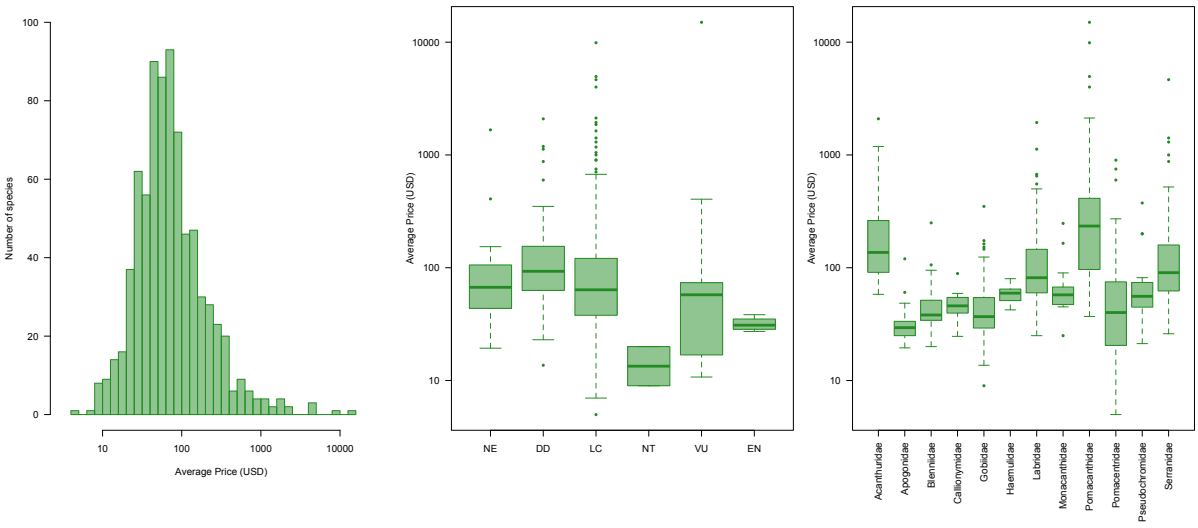

Figure 3.2: *Average prices of the fish species assessed in this study and price variability by IUCN threat status and taxonomic family. Leftmost panel uses log scale for x-axis retail price.*

Finally, we found that 58 species in our dataset had specimens sourced both from the wild and through captive breeding. When we compared the prices between these wild-caught and captive-bred conspecifics (of the same color morphs), we found that the captive-bred individuals were cheaper for 41 of the 58 species (70.7% of the species analyzed). This

reduction was significant across all paired samples (paired t-test, t = -2.5, p = 0.015) and led to a 23.2% ± 18.1 (mean ± 95% confidence interval) reduction in price (Figure 3.4).

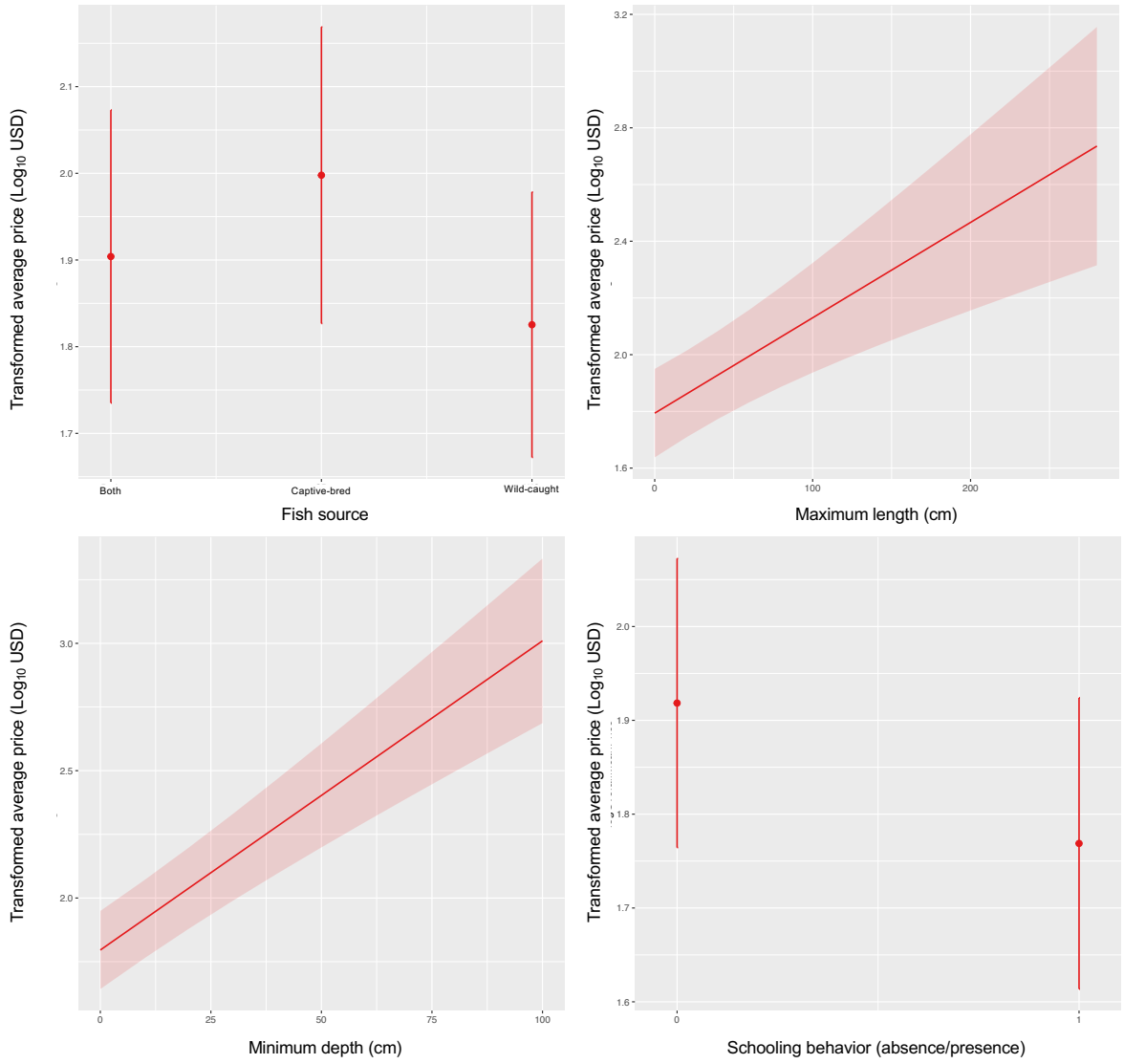

Figure 3.3: Marginal effects plots for fish source, maximum length, minimum occupied depth, and schooling behavior.

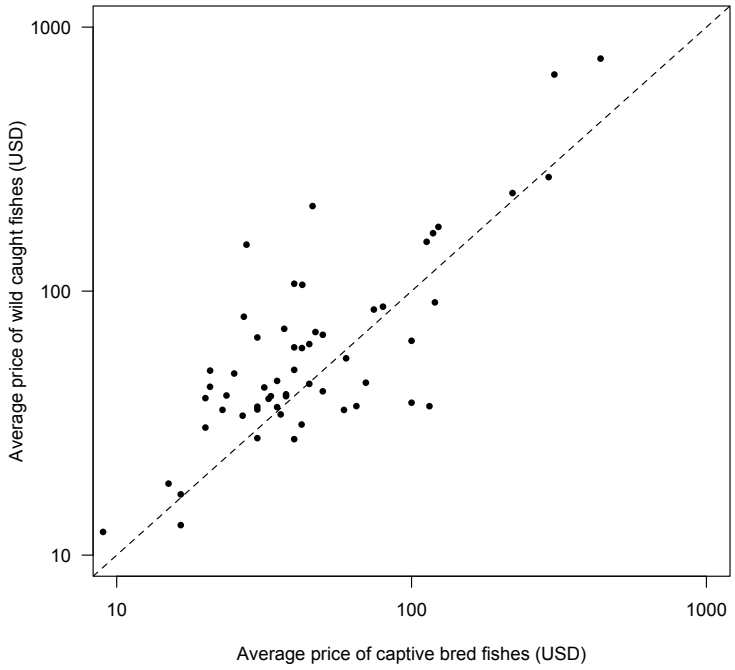

Figure 3.4: Fish prices for specimens that were available as both captive-bred and wild-caught. Points above the dotted y = x line are listings where captive-bred specimens were cheaper than their wild-caught counterparts.

3.4: Discussion

Here, we provide a contemporary snapshot of the online ornamental marine fish trade across the United States, and we assess the implications of this trade for conservation.[120] Of the 660 species of marine fish sold across four major e-commerce platforms, 153 species were previously not recorded as being of commercial interest or as sold in the aquarium trade according to either the IUCN or Fishbase, two authoritative databases of wild fish species. We also found 88.9% of the 660 species sold to be sourced from wild populations, although we note that this determination is based on the self-reporting of online retailers. Any errors in

reporting, either accidental or intentional, could affect our results, although we have no reason to suspect systematic biases in self-reporting.

This heavy reliance on wild-caught fish populations could increase anthropogenic pressures within the habitats from which these hundreds of fish species are caught. Typically, marine ornamental fish are captured in developing countries in the tropics, such as Indonesia and Philippines,[111] where their capture has historically (but not invariably) been linked to unsustainable or untargeted forms of fishing, including cyanide and blast fishing.[110,115,122] Considering the high rates of both direct and indirect mortality through the marine ornamental trade supply chain,[109] rising consumer demand will likely trigger additional and outsized levels of wild capture, especially in the absence of policy or community reforms around sustainable fisheries or viable alternative means of sourcing.

Retail prices were also strongly associated with indicators of accessibility and ease of capture. For instance, we found that smaller, schooling fishes occupying shallower depth ranges tended to be cheaper. When lower prices trigger commensurate increases in demand, this can put many ecologically similar species at risk, especially given the expansive demand for marine ornamental fish across multiple taxonomic families (Figure 3.1).[110] Developments in harvesting techniques or technologies would also expand the suite of fish species accessible for capture, simultaneously reducing prices and raising demand.

Looking across all species that are sold, our mixed effects models found that wild-caught species tended to have cheaper prices than captive-bred species. This could be problematic if at-risk species are readily accessible in the market; it also suggests that species' extinction risks might be a market externality that is not fully captured in online retail prices at the present

time. Conversely, for the 58 species in our dataset that had both captive-bred and wild-caught specimens for sale, pairwise comparisons found captive-breeding to generally yield cheaper prices than wild capture. This suggests that for some species, transitioning to captive breeding has the potential to help species conservation without hindering market supply or price. Additional factors in consumer preference and market demand could also drive this price differential, such as the availability of diverse wild-caught species acting as market competition (to reduce prices), as well as the up-front and overhead costs of establishing and maintaining captive breeding programs, and the required equipment and requisite research and development to do so, especially in higher-waged, developed countries.[118]

The persistence of more expensive, wild-caught counterparts in the trade when captive-bred individuals are available might point to a preferential premium placed by hobbyists on owning wild-caught fish, either as a product of greater phenotypic diversity, perceived differences in resilience or attractiveness of such fish, or other factors. A similar preference for wild-caught versus captive-bred songbirds on the part of some pet owners has been noted in Indonesia.[123] This could also be a reason why there were only 25 species sold exclusively through captive breeding. For instance, the Banggai Cardinalfish (*Pterapogon kauderni*) is a highly prized aquarium species endemic to Indonesia and classified as Endangered by the IUCN. It is primarily sourced from the wild despite successful captive breeding programs.[124,125] In our data, wild-caught Banggai cardinalfish fish sold for $39.99 USD, while captive-bred Banggai cardinalfish sold for $37.52 USD. At least in some cases, the availability of cheaper, captive-bred equivalents to wild-caught fish might not be sufficient to wholly erase the trade in

wild individuals. Additional efforts, such as social-media campaigns in support of owning captive-bred fish, may be needed.

Sustainable fisheries are crucial for the marine aquarium trade, as they provide a means of sourcing fish without exacerbating the pressures on wild populations. Responsible management practices can also help ensure that commonly traded fish species are harvested in ways that reduce bycatch, minimize habitat destruction, and maintain ecosystem equilibrium. Furthermore, sustainable fisheries can promote economic stability for local fishing communities while alleviating the reliance on wild capture, ultimately contributing to the conservation of threatened species and the habitats they depend on.[118,126]

Additionally, captive breeding, in lieu of unsustainable wild capture, might be a commercially viable path forward for conservation, especially for species already experiencing elevated levels of extinction risk.[110] Shifting to captive propagation could not only alleviate exploitation pressures placed on wild populations of target species but could also reduce the bycatch of non-target species and the ecological damages associated with destructive fishing methods. Due to the environmental and reproductive barriers that must be overcome for successful captive breeding, however, not all species are suitable for such strategies.[109,127] As such, priority should be placed on the marine ornamentals with both high consumer demand and high extinction risk and should be accompanied by behavioral interventions aimed at shifting consumer demand towards sustainably-sourced species, a process in which public aquariums could help to play an important role.[128]

Importantly, the consequential impacts to local community suppliers that a switch to aquaculture might entail must not be overlooked. This is especially important when desirable

species become increasingly difficult to source in the wild, both from overexploitation and reef degradation.[118] Therefore, promoting a sustainable marine aquarium trade in wild fish, possibly through carefully implemented certification schemes,[129] might be viable options for conservation that are complementary to sustainable captive propagation. With all approaches, adequate information, adaptability, and oversight are key to ensuring the long-term viability of reef ecosystems and the many communities that depend on them.[126]

Currently, it appears that the aquarium trade has heretofore had a relatively minor impact on the extinction risks of most marine ornamental species, given that 97.6% (573 of 587) of wild-caught species are not currently classified as imperiled by the IUCN. However, we identified 20 threatened species sold, according to the IUCN (4 Endangered species and 16 Vulnerable species), and an additional 19 species with population trends assessed by IUCN as decreasing. Of these 39 species with elevated conservation concern, 82% were sourced exclusively from wild populations. For this highly lucrative yet understudied component of the global wildlife trade, policymakers clearly need a much firmer understanding of the ornamental marine fish trade's true size and scale, both in the United States and beyond. This includes the trade's effects on local economies along all nodes of its global supply chain and on the reef ecosystems where the fish are obtained. With this knowledge, policymakers will finally be able to craft regulations that can successfully protect vulnerable fish species while also ensuring the economic and environmental well-being of coral reefs and the millions of people that depend on them.

Acknowledgements

We thank Princeton University and the High Meadows Foundation for ongoing support of our work. The authors declare no competing interests.

Data Availability

The web-scraped data we used in our study are available in this Zenodo repository: https://zenodo.org/doi/10.5281/zenodo.10688436, which has also been populated with columns extracted from the publicly accessible Fishbase and IUCN databases.

Appendix

A3.1: Online dealer inclusion criteria

To evaluate aquarium dealers for inclusion, we used a variety of Google search terms to find dealers that were the most comprehensive and accessible to consumers. Candidate search phrases included keywords such as “Aquarium”, “Saltwater”, and “Coral Reef”, which were paired with sale-related keywords such as “Trade”, “Dealer”, and “For Sale”. Our final search parameters were "Saltwater Coral Reef Fish For Sale", which produced a list of candidate dealers that were further narrowed to include e-commerce platforms that had saltwater fish for sale with accessible pricing information and navigable user interfaces. Private browsing modes were used to minimize possible location-dependent biases in search results.

The search parameters produced a list of ten suitable dealers in July 2021, with Live Aquaria serving as the benchmark due to its extensive inventory offering over 900 unique fish phenotypes. Live Aquaria also self-reports as the largest online retailer for fish in the United States on their website, which was subsequently confirmed through phone communication with an employee. Of our ten candidate dealers, only four were comprehensively comparable in the breadth and volume of marine fish diversity sold: Live Aquaria, Blue Zoo Aquatics, Saltwaterfish.com, and That Pet Place.

As an additional benchmark to ensure that our chosen dealers were a fair representation of the scope of the online ornamental marine fish trade in the United States, we created a rarefaction curve of unique species accrued as a function of each additional dealer we sampled. Wild-caught and captive-bred conspecifics, as well as intra-species phenotypic diversity, were pooled and treated as a single species (Figure A3.1).

Of the 12 *Actinopterygii* families chosen for study inclusion, Blue Zoo Aquatics had 497 unique species for sale, Saltwaterfish.com had 456 unique species for sale, Live Aquaria had 365 unique species for sale, and That Pet Place had 349 unique species for sale. Between dealers, this represents a tapering increase in unique species from 19.11% (95 additional species when adding a second dealer), to 5.41% (32 additional species from adding a third dealer), to 5.77% (36 additional species from adding a fourth dealer) respectively—a total of 660 unique species overall. (These numbers do not reflect the total species or phenotypic inventory for each dealer, nor do they indicate the volume of specimens sold for each species.)

A3.2: Taxonomic family inclusion criteria

The twelve *Actinopterygii* families chosen for this study were those with the most species available for sale across all four dealers. Inclusion criteria for taxonomic families included those that had at least 30 unique species for sale [seven families: *Labridae* (Wrasses), *Pomacentridae* (Clownfishes, Damselfishes, Chromis), *Gobiidae* (Gobies, Dartfishes, Firefishes), *Serranidae* (Anthias, Basslets, Basses, Groupers), *Pomacanthidae* (Angelfishes), *Acanthuridae* (Tangs), and *Blenniidae* (Blennies)], as well as taxonomic families that contained any number of captive-bred specimens for sale [five families: *Apogonidae* (Cardinalfishes), *Callionymidae* (Dragonets), *Monacanthidae* (Filefish), and *Haemulidae* (Grunts, Sweetlips, Porkfish)]. As online dealers differentiate by common name rather than by

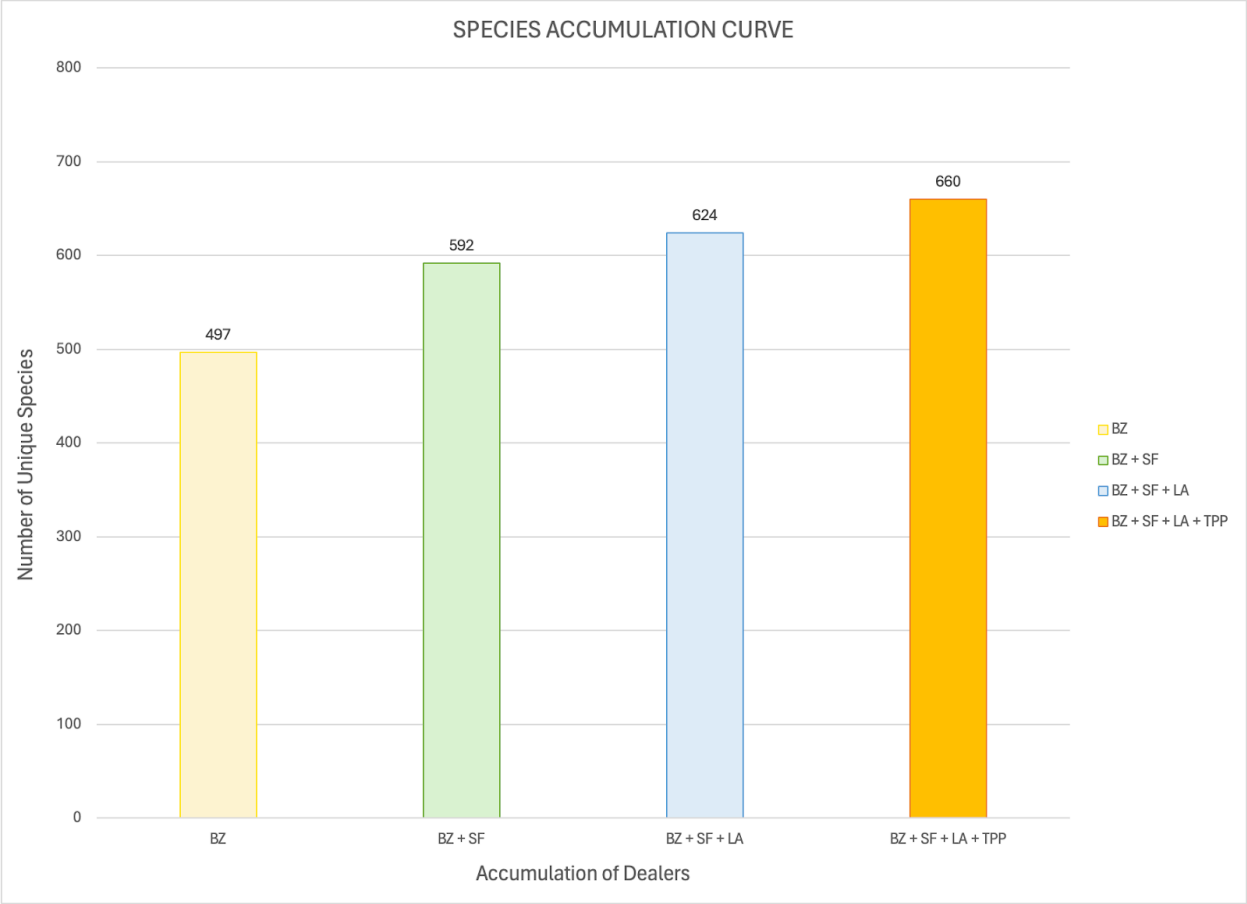

Figure A3.1: Species accumulation curve between dealers. BZ = Blue Zoo Aquatics; SF = Salfwaterfish.com; LA = Live Aquaria; and TPP = That Pet Place.

scientific name (for instance, Live Aquaria sells Clownfish, Damselfish, Angelfish, and Blennies all on different webpages), fish specimens were manually sorted by taxonomic family ex-post.

A3.3: FishBase and IUCN trait data

We extracted a host of ecological and economic fish trait data from both FishBase and IUCN. For IUCN, we downloaded the "Range data - Points (CSV)" under the *Actinopterygii* criterion. We manually coded the “Habitat and Ecology” text into discrete fish life history traits. For Fishbase, we downloaded the “Species” data from the “rfishbase” library in R and

manually coded the text from the "Biology" and "Life Cycle and Mating Behavior" sections into separate trait columns.

Across both Fishbase and IUCN, traits included each species' IUCN threat status, maximum length (cm), geographic origin (Pacific Ocean, Atlantic Ocean, Indian Ocean), minimum depth (m), maximum depth (m), vertical column location (pelagic, demersal benthopelagic, demersal benthic), eggs (pelagic, demersal), larvae (pelagic, not pelagic), diet (herbivore, carnivore, omnivore, detritivore), sexual dimorphism (binary), hermaphroditism (gonochoristic, simultaneous, protogynous, protandrous), grouping (singly, pairing, schooling), breeding (pair breeding, spawning aggregation, mouthbrooding), mating (monogamy, haremic, polygamy), territorial or aggression, longevity (years), diurnal or nocturnal, and anemone association (binary).

A3.4: Correlates with retail prices

Linear mixed effects models were used to evaluate a total of 17 competing hypothetical models within an information theoretic framework (see Table A3.1). These 17 models were selected based on a combination of availability of FishBase and IUCN trait data, and potential contributions of various species traits to retail price. Both fish family and IUCN threat status were treated as random effects in our study (see Table A3.2 for summary statistics). We used the following species traits as fixed effects based on their potential links to ornamental trade desirability, importation volume or price—maximum length, dietary preferences, schooling behavior, geography, minimum occupied ocean depth, occupied depth range, and fish source (Winemiller, 2005; Smith et al. 2008; Rhyne et al. 2012). Model performance was evaluated with Akaike information criteria corrected for small sample sizes (Table A3.1).

Table A3.1: Full linear mixed effects model list and performance evaluation

Model	Fixed effect variables	Degrees of freedom	AICc	ΔAICc
1	maximum length, minimum occupied ocean depth, geography, fish source, dietary preferences, schooling behavior	15	510.3	3.4
2	maximum length, occupied depth range, geography, fish source, dietary preferences, schooling behavior	15	563.3	56.4
3	maximum length, minimum occupied ocean depth, geography, fish source, dietary preferences	14	538.4	31.4
4	maximum length, occupied depth range, geography, fish source, dietary preferences	14	597.2	90.3
5	maximum length, minimum occupied ocean depth, geography, fish source	12	540.4	33.5
6	maximum length, occupied depth range, geography, fish source	12	602.4	95.5
7	maximum length, minimum occupied ocean depth, geography, fish source, schooling behavior	13	509.5	2.6
8	maximum length, occupied depth range, geography, fish source, schooling behavior	13	564.9	58.0
9	maximum length, minimum occupied ocean depth, fish source, dietary preferences, schooling behavior	11	509.0	2.0
10	maximum length, occupied depth range, fish source, dietary preferences, schooling behavior	11	571.1	64.2
11	maximum length, minimum occupied ocean depth, fish source, dietary preferences	10	534.5	27.5
12	maximum length, occupied depth range, fish source, dietary preferences	10	602.3	95.4
13	maximum length, minimum occupied ocean depth, fish source	8	535.0	28.1
14	maximum length, occupied depth range, fish source	8	605.7	98.8
15	maximum length, minimum occupied ocean depth, fish source, schooling behavior	9	506.9	0.0
16	maximum length, occupied depth range, fish source, schooling behavior	9	571.4	64.5
17	null model	4	587.5	80.6

Table A3.2a: Ornamental marine fish price summary statistics by IUCN threat statu s

IUCN status	Number of species	Mean	95% confidence interval	Min	Max	25% quantile	Median	75% quantile
Not Evaluated	24	149.91	133.08	19.35	1668.79	44.32	67.13	103.99
Data Deficient	35	255.79	143.42	13.66	2090.99	62.99	92.99	154.99
Least Concerned	702	153.47	37.68	4.99	9882.49	37.70	63.64	120.37
Near Threatened	2	14.49	10.78	8.99	19.99	11.74	14.49	17.24
Vulnerable	17	962.27	1720.50	10.74	15000.00	16.87	57.57	73.66
Endangered	4	31.89	4.66	27.24	38.35	29.16	30.98	33.70

Table A3.2b: Ornamental marine fish price summary statistics by taxonomic grouping

Family	Number of species	Mean	95% confidence interval	Min	Max	25% quantile	Median	75% quantile
Acanthuridae	58	233.23	79.53	58.12	2090.99	92.23	136.62	261.06
Apogonidae	21	35.23	9.26	19.49	119.99	24.99	29.44	33.49
Blenniidae	44	48.74	10.67	19.99	249.99	34.32	38.11	49.93
Callionymidae	8	49.31	13.14	24.64	88.88	40.67	46.08	52.47
Gobiidae	92	50.45	9.04	8.99	349.99	29.34	36.87	54.15
Haemulidae	8	59.18	8.12	42.32	79.99	51.74	59.52	62.43
Labridae	179	136.25	27.54	24.99	1939.55	59.91	81.56	145.71
Monacanthidae	15	75.28	28.88	24.99	247.16	47.26	57.49	67.49
Pomacanthidae	73	797.05	497.44	36.99	15000.00	96.52	234.32	412.72
Pomacentridae	189	63.74	14.17	4.99	898.99	20.49	39.99	74.32
Pseudochromidae	23	79.41	32.25	21.24	374.99	44.74	55.79	73.99
Serranidae	74	233.84	132.17	25.99	4649.99	62.53	90.43	158.13

Chapter 4 — The co-dependence of coral reefs and coastal tourism at the archipelago scale

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Abstract

By combining web-scraped social media (Instagram) data from tourists and high-resolution live coral cover maps across the main Hawaiian Islands, we present first evidence of coral reefs systematically attracting and suffering from coastal tourism at a regional scale. Higher average and total live coral cover attract increased rates of on-reef visitation specifically, but that visitation contributes to the subsequent degradation of those reefs. This results in feedback loops that selectively threaten the highest-quality reefs, underscoring both the value of coral reefs to tourism and the exigency of their conservation.

4.1: Main

Coral reefs are exceptionally rich in marine species and provide vital ecosystem services for humanity. Yet, they are also on a steep and sweeping global decline due to climate change and local anthropogenic stressors.[11] Tourism has been cited as a promising way to reduce local reef threats by fostering non-extractive livelihoods and generating funds for reef conservation and sustainable development.[130] Indeed, tourism features heavily in the UN 2030 Agenda for Sustainable Development goals and is identified as a means to promote the sustainable future use of marine and coastal resources (Goal 14).[131]

However, tourism can also be harmful to reefs. Specifically, coastal visitation can indirectly impact reefs through tourism-related development and pollution,[132] and on-reef activities such as snorkeling and scuba diving can directly damage individual coral colonies.[133] Difficulties in collecting accurate and expansive data on where tourists travel and their associated reef impacts mean that a systematic understanding of how live coral relates to tourism remains poorly known. Existing studies are typically restricted to just a few sites,[134,135] or they rely on course-scale approximations of where and how coral reefs and tourism are distributed.[136]

Here, we leverage social media data and the popularity of Instagram to quantify coastal tourism across the main Hawaiian islands, and compare visitation rates with various indicators of live coral cover, water condition, human activity, and site accessibility, using a new and very detailed map of coral cover.[137] We use a high-resolution geospatial approach to determine (a) the fine-scale relationship between reef conditions and both overall and on-reef coastal tourism, and (b) whether site-specific direct and indirect impacts of tourism on live coral are systematically detectable at a regional scale.

Social media data are an accurate and expansive proxy for nature-based tourism and recreation across a broad expanse of natural systems,[130,138–143] including for on-reef and overall coastal tourism,[144] and Instagram posts *per se* demonstrably outnumber and outperform other types of social media platforms as a reliable, modern proxy for tourist visitation (see Appendix for details, validation, and limitations; Figure A4.1).[141,145] Further, Hawaii is an ideal locale for such a study because public access to the shoreline is a common law right, and most coastal sites are readily accessible by road and have cellular connectivity to facilitate real-time visitation updates.[146,147] Moreover, most tourists in Hawaii are "free independent travelers", meaning they are not beholden to packaged-tour itineraries. Thus, visitation data in Hawaii reflect where tourists wish to be rather than just where they are allowed to be.

From 2018 to 2021, 275,724 public posts (photo-user-days) were uploaded to Instagram across 333 bays and beaches in the main Hawaiian islands (see Methods and SI for details and inclusion criteria).[138] We attributed 9,231 of these posts to on-reef visitation via caption and hashtag searches of reef-related keywords.[144] Overall, we find that higher rates of coastal visitation are associated with increased site accessibility, as indicated by hotel density and distance to the nearest road, and also associated with increased nearshore effluent (R^2 = 0.72 ± 0.15; RMSE = 0.08 ± 0.02) (Figure 4.1). In comparison, sites with higher rates of specific on-reef visitation are linked to greater accessibility, indicated by hotel density, but also with higher total and average live coral cover and better water quality (R^2 = 0.83. ± 0.05; RMSE = 0.07 ± 0.01) (Figure 4.1).

The understanding that both average and total live coral cover drive on-reef visitation is crucial to spatially explicit quantifications of how coral reefs can facilitate coastal economic

growth through tourism, and dovetails with existing research integrating ecosystem services into marine and coastal planning.[130,148] Furthermore, the role of site accessibility in driving both overall and on-reef visitation, a finding also replicated in other nature-based tourism studies,[130,149] underscores an important trade-off when prioritizing between development and the environment. While accessibility is important to visitation, it necessarily requires infrastructure development, often to the detriment of the very ecosystems to which tourists want access. Thus, that on-reef tourism is systematically driven by both better reef and water quality across hundreds of sites (Figure 4.1) provides opportunities for synergies in coastal management to benefit both reef ecosystems and the economy.

At the most popular sites, we also find a strong positive correlation between overall visitation and absolute live coral cover (Figure A4.2). However, the most popular sites also show evidence of live coral cover suppression close to shore (where tourism is most concentrated) compared to less popular sites, even after controlling for depth ($W_{\text{Mann-Whitney}}$ = 689, p = 0.006) (Figure 4.2) (see Methods and SI). These findings suggest that while live coral might attract visitors, that visitation is also stifling live coral cover right by the shore, an impact that attenuates farther into the water (Figure 4.2). Acute mechanisms through which tourists damage corals are well documented, and include reef contacts and trampling by divers and snorkelers,[133,150] and chemical pollutants, such as sunscreens, from swimmers.[151] Conducting this same analysis between more- and less-polluted sites yielded null results ($W_{\text{Mann-Whitney}}$ = 465, p = 0.867), suggesting that it is visitation, not nearshore effluent, that is contributing the most to coral degradation at this scale of analysis (see Methods and SI).

These findings also introduce nuance into the debate as to whether local and global reef stressors are synergistic actors in the coral reef crisis.[152] Studies dismissing local stressors as meaningful contributors to coral loss often draw their conclusions from the absence of a relationship between live coral cover and localized anthropogenic stressors.[153–155] However, we were able to detect negative visitation impacts only by using meter-scale comparisons of live coral cover across a visitation gradient. These impacts would have escaped detection at coarser scales of analysis, thereby demonstrating the value of high-resolution data in revealing certain types of reef threats.

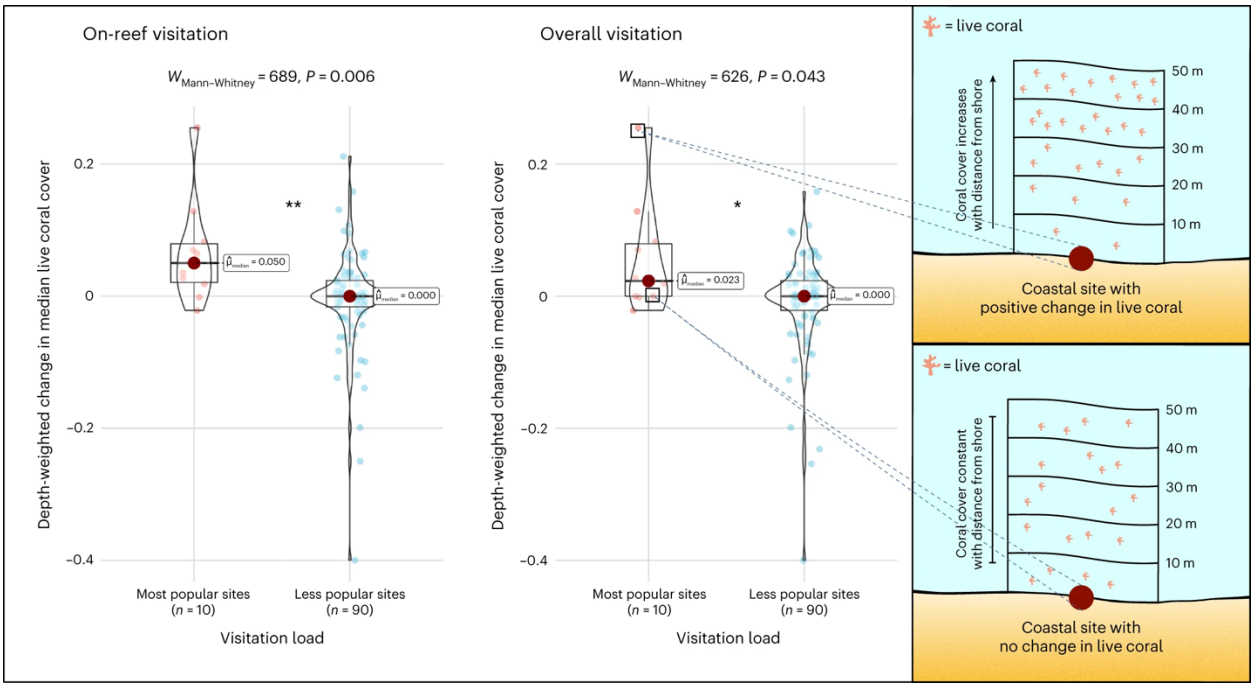

Figure 4.2: The change in live coral cover with increasing distance from shore between more and less popular sites in Hawaii for on-reef and overall coastal visitation. Left panel: the depth-weighted change in median live coral cover with increasing distance from shore for on-reef and overall coastal visitation across the most popular 100 coastal sites in Hawaii. The whisker plot midlines represent the median values, the boxes represent the interquartile range, and the whiskers extend to the minimum and maximum values. (The two-sided Mann–Whitney U-test results remain significant with outliers removed.) Right panels: schematics for how the change in live coral cover was calculated from 0 to 50 m away from shore at each coastal site. The top right panel depicts a site with a positive gradient and the bottom right panel depicts a site with no gradient (live coral cover remains constant with increasing distance from shore).

Overall, our study provides novel evidence that live coral cover is both a driver of, and victim to, coastal visitation at a large scale. Pernicious impacts of visitation and negative feedback loops selectively threaten the highest-quality reefs. Although high-quality reefs attract more tourists, that tourism can contribute to the degradation of those reefs. Furthermore, the large overlap between popular sites for overall and on-reef visitation (80% overlap for the top 50 sites; Figure A4.3) has clear management implications: these visitation hotspots are simultaneously under threat from both the indirect effects of overall visitation (e.g., increased effluent levels; Figure 4.1) and also from the direct impacts of on-reef visitation (Figure 4.2), and are therefore doubly at risk of further degradation.[156] Conservation efforts must include strong reef-protecting policies and additional reef restoration measures, especially at sites with high visitation (Table A4.1; Table A4.2). Yet, coastal and marine management should also better account for the positive role of live coral in attracting tourists; sustainable development planning must grapple with complex trade-offs between the environment and economy.[148] Ultimately, if coastal tourism is to be an effective step towards sustainable growth for the many millions of people who rely on coral reefs for their lives, livelihoods, or leisure, we must better understand the intricate and inter-related relationships between coral-reef health and tourism, not just in Hawaii but wherever these vanishing ecosystems occur.

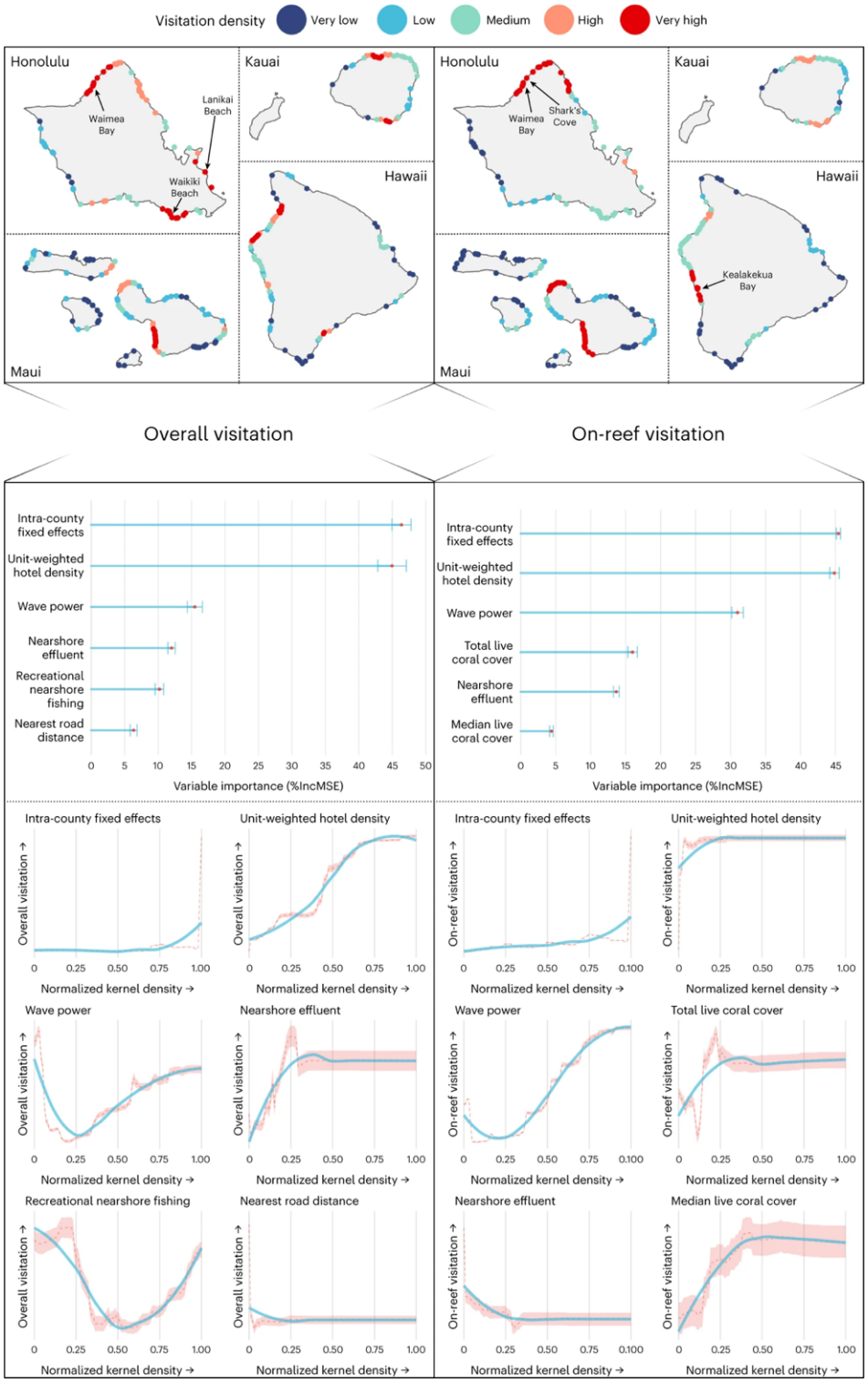

Figure 4.1: *The relative distributions and drivers of on-reef and overall coastal visitation across the main Hawaiian Islands. Top panels: relative coastal visitation intensities across the main Hawaiian islands, with the three most visited sites for overall and on-reef tourism labelled. Bottom panels: relative contributions of the most important variables associated with on-reef and overall coastal visitation based on random forest regression models, and their corresponding partial dependence plots. Error bars depict 95% CI of 100 bootstrap samples in the variable importance plots. Dotted lines depict partial dependencies, shaded regions depict 95% CI of 100 bootstrap samples, and blue lines depict LOESS smooth curves in the partial dependence plots.*

4.2: Methods

We used the Selenium WebDriver package in Python to quantify coastal tourism by web-scraping across 333 bays and beaches in Hawaii that (a) were situated within 10,000 m of a paved road, (b) had geotagged Instagram identifiers, and (c) had live coral cover data within a 1,000 m by 100 m buffer area (see Appendix; Figure A4.4).[157] For every public Instagram post, we collected metadata on location, time, caption, hashtag, and username content, and operationalized on-reef visitation by subsetting for posts containing internally validated, reef-related keywords (see Appendix).[144] We converted total post counts to photo-user-days (one post per username per day at each site) to account for discrepancies in post frequency between users,[138] and truncated our analysis to only non-retrospective posts uploaded between 2018 and 2021 (definition and details in the Appendix). Finally, to avoid skewed Instagram-derived visitation rates stemming from geographic proximity between sites, we converted photo-user-days at each site into a raster of kernel densities for both overall and on-reef visitation.

We used an airborne mapping process coupling laser-guided imaging spectroscopy with artificial neural networks to quantify live coral cover at a 2-meter resolution to a 16 m depth across the main Hawaiian Islands.[137] We calculated zonal statistics for live coral cover, water depth, and additional variables on nearshore human activity, site accessibility, and water conditions at each site obtained from the Ocean Tipping Points project and the Hawaii Statewide GIS Program (Table A4.3).[158,159]

We normalized all candidate features and used machine learning random forest models to assess the contributions of live coral cover and other variables to overall visitation and on-reef visitation (Figure 4.1, Table A4.4). A random forest regression approach was chosen for its robustness to skewed and non-linear datasets while retaining high accuracy and efficiency,

and for its reliability in other studies involving shallow reef habitat mapping.[160,161] We computed each feature's variable inflation factor, mean decrease accuracy (%IncMSE), and partial dependence plots using bootstrapped 95% confidence intervals, and compared each model's R^2 and RMSE between training and testing datasets (split at 0.7) using the "Boruta", "regclass", and "Metrics" packages in R 4.1.2.

To estimate intra- and inter-site impacts of visitation on live coral cover, we calculated the depth-weighted change in live coral cover from 0 to 50 m away from shore at each site and compared this gradient between more- and less-visited sites for both on-reef and overall visitation (see Appendix). As visitation is usually most concentrated right at and close to shore, calculating the change in live coral cover at increasing distances from shore allows for an intra-site assessment of visitors' impacts on live coral cover. Relative to absolute comparisons of live coral cover, this gradational approach accounts for both site-specific differences in live coral cover (e.g., impacts of natural embayments and artificial dredging), as well as simultaneous causality (i.e., when live coral synchronously attracts visitors yet suffers coastal visitation). We compared the change in live coral cover between high and low visitation sites using non-parametric Mann-Whitney U tests, repeated this analysis for high and low pollution sites to test for nearshore effluent as a potential confounder, and conducted randomization inference procedures using randomly assigned site visitation rankings in a Monte Carlo simulation (10,000 runs) to test for model misspecification (see Appendix).

Data Availability

The Instagram social media dataset generated and analyzed during the current study will be available in the Zenodo repository with all accession codes before publication. The live coral

cover data are available in the Zenodo repository, http://doi.org/10.5281/zenodo.4292660. The human activity, site accessibility, and water conditions data are available through the Ocean Tipping Points project, http://www.pacioos.hawaii.edu/projects/oceantippingpoints; and the Hawaii Statewide GIS Program, https://geoportal.hawaii.gov/.

Code Availability

All R and Python scripts used to process the data are available from the corresponding author upon request.

Acknowledgments

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Appendix

A4.1: In-Depth Methodology

A4.1.1: Procuring and processing Instagram-based visitation data

To provide an expansive yet accurate estimate of human visitation across coastal sites, we used social media (Instagram) data as a proxy for on-reef and overall visitation. Geotagged social media posts provide a reliable estimate of otherwise difficult-to-obtain visitation information across myriad natural systems,[130,138–143] and Instagram specifically has experienced explosive growth in recent years to become the most data-rich, photo-based social media platform in the world. (As of December 2021, Instagram has over two billion active users worldwide and over 150 million active users in the United States alone.)[162]

We used the "geonames" dataset compiled by the U.S. Geological Survey (USGS) to extract the names and coordinates of 683 bays and beaches in the state of Hawaii.[163] Next, we wrote a Python script using the Selenium WebDriver package to cross reference each USGS site name with its corresponding Instagram location page, where available, and manually validated all sites that had multiple, duplicate, or conflicting names. We also used the Selenium WebDriver package to scrape through each Instagram-validated location webpage and to collect content information on all public posts geotagged at each coastal site, including data on the post account user, upload time and day, caption, and hashtag content (code adapted from Volenec et al., 2021).[164] We further processed these raw post counts in several ways:

1. We limited our study to Instagram posts uploaded between January 1 2018 and December 31 2021.

2. We converted raw post counts into photo-user-days, defined as the total number of days across all users that each person uploaded at least one photo/video at each coastal site (sensu Wood et al., 2013).[138] Converting raw post counts to photo-user-days helps to account for discrepancies in upload frequency between users, and was operationalized by subsetting for only one post per Instagram username per day at each coastal site.
3. We excluded retrospective posts, which are uploaded in reference to past events or experiences that are not representative of actual visitation. This was done by removing posts containing the keywords "flashback", "throwback", or "tbt" (throwback Thursday) in their caption or hashtags.
4. We limited our analysis to coastal sites containing live coral within a 1,000 m by 100 m buffer (1,000 m along the shoreline and 100 m extending into the ocean) (Figure A4.4). This helped to exclude inlets and harbors (e.g., Pearl Harbor) from consideration.
5. We excluded sites that were farther than 10,000 m from the nearest road, as such sites are likely inaccessible for most visitors to Hawaii (e.g., sites on Niihau island, Kauai).

We estimated o n-reef visitation by subsetting for posts containing the keywords "coral", "reef", "snorkel", "scuba", "underwater", and "padi dive" in eight languages: English, Dutch, French, German, Italian, Spanish, Chinese, and Japanese (methods adapted from Spalding et al., 2017).[144] However, we began with a list of general reef-related keywords, including the common, Latin, and Hawaiian names of common Hawaiian reef fish (40 species),[165] marine mammals (11 species),[166] and reef-building coral and algae species (9 species),[167] and removed

keywords based on both their relative contributions to bolstering the on-reef visitation data and on how well their post content represented on-reef visitation, performed through visual inspections of random posts containing each keyword candidate. Many reef-related keywords, such as "fish", were removed due to definitional conflicts or ambiguities (e.g., pictures of fish, fishing, and fish-based food items). Hence, we ended up with the six keywords above.

After collecting our post data, we validated these results with on-the-ground visitation data obtained from the Hawaii Tourism Authority.[168] Overall, these county-level, daily census data correlated well with our Instagram post counts for all years spanning 2018 to 2021 (Figure A4.1). Because geographic proximity between sites might skew visitation rates, we subsequently projected all point and raster values to the Hawaii Albers Equal Area Conic map in ArcGIS Pro 3.0, converted each site's post data into a raster of kernel densities at a 10 m scale for both overall and on-reef visitation, and interpolated and extracted visitation density values for each site.

A4.2.2: Limitations of social media- and Instagram-derived visitation data

Despite the above adjustments to our dataset, there are inherent limitations to using social media-based data as a proxy for human visitation based on introduced biases stemming from who uploads what pictures, to which online platforms, at what locations, and involving what activities.[138,142,169] And specific to using Instagram posts to estimate coastal visitation in Hawaii, several additional assumptions and limitations arise. Accordingly,

1. This analysis was limited to public Instagram posts, which means that the subset of posts extracted for subsequent analysis was only a small proportion of total Instagram

post uploads, since no data from private posts or temporary "Instagram stories" were collected. Fortunately, the high volume of overall active Instagram users ensured a large sample size across sites (our cleaned dataset had over 250,000 posts across 333 bays and beaches). Also, we chose to assess rates of relative visitation across sites (after converting photo-user-days to kernel densities; see above) instead of total post counts, thus providing accurate comparisons of visitation across sites that should not be affected by the missing data (assuming that the visitation preferences of public and private account users are by and large comparable).

2. In- and under-water experiences are difficult to photographically capture, which might reduce the sample size of relevant posts describing on-reef experiences. Indeed, this is likely a reason why less than 10,000 of over 250,000 photo-user-days were reliably attributed to on-reef visitation in our analysis. Thus, to obviate access to underwater photography equipment as an exclusionary constraint, we quantified on-reef visitation through reef-related keywords extracted from photo captions and hashtags (see above), which allowed tourists referencing on-reef experiences to be classified as an on-reef visitor, without necessarily needing to have taken an underwater photo.
3. Instagram data rely on user-specified location information, which means that posts uploaded may not necessarily reflect exactly where and when each picture was actually taken. While this limitation applies to nearly all social media platforms, we estimate that only a small proportion of Instagram posts are likely to be incorrectly tagged across Hawaii. This is because most of the main Hawaiian islands have full mobile LTE

coverage (with nearly 100% coverage across coastal sites), resulting in wide-ranging access to the internet and online location services.[147]

4. There are likely substructure effects involving Instagram users; namely, distributional biases toward younger and more technologically-inclined people (e.g., two thirds of Instagram users are 34 years or younger as of April 2022).[162] While this skewed representation of the population is an inherent limitation of using Instagram data, given the hundreds of millions of global Instagram users, the wide distribution of visitor ages in Hawaii (e.g., 59% of visitors to Hawaii were 40 or younger in 2021),[168] and given the likelihood of non-Instagram users traveling in the same party as Instagram users (e.g., a family trip), there is likely enough overall overlap in the distribution of actual and Instagram-derived visitation to provide an accurate picture of where tourist crowds cluster (Figure A4.1). (However, this limitation does speak to the benefits of using visitation data derived both from social media aggregation and on-site counts.)[139]

A4.2.3: Live coral cover and additional variable processing

To estimate live coral cover, we used an airborne mapping process coupling laser-guided imaging spectroscopy with artificial neural networks to quantify live coral cover distributions at a 2-meter resolution to a 16 m depth across the main Hawaiian Islands (methods detailed in Asner et al., 2020).[137] We obtained additional variables from the Ocean Tipping Points project and the Hawaii Statewide GIS Program, broadly classified into three categories: site accessibility, human activity, and water conditions (Table A4.3).[158,159]

For each bay and beach, we computed the nearest point on the shoreline and delineated a buffer area of 1,000 m along the shoreline by 100 m into the ocean at each site (Figure A4.4). In each buffer, we calculated zonal statistics for live coral cover, water depth, and all additional human activity, site accessibility, and water condition variables (Figure A4.3). We kept two metrics of live coral cover in our models: median and total live coral cover, as these represent related yet distinct aspects of reef quality with relatively low variable inflation factors (~4).

A4.2.4: Random forest model and feature selection

To assess drivers of visitation, we normalized all candidate features and used the "randomForest" package in R 4.1.2 to run random forest regressions for on-reef and overall visitation using intra-county standard topographic map names to account for intrinsic regional-level differences in visitation. Random forest regressions are a powerful ensemble learning approach that is well-suited for large and incomplete datasets. They operate without assumptions of linearity and provide means for model cross validation between training and testing datasets.

To determine each feature's suitability for model inclusion, we assessed each response variable's inflation factor, mean decrease accuracy (%IncMSE), partial dependence plot, and performance relative to random noise using bootstrapped 95% confidence intervals, as well as each model's R^2 and RMSE compared between training and testing datasets (split at 0.7) using the "Boruta", "regclass", and "Metrics" packages in R 4.1.2.

A4.2.5: Gradational impacts of visitation across coastal sites

To assess visitation impacts on live coral cover across a gradient of human visitation, we created 1,000 m by 10 m buffer strips parallel to the coastline at each site, stacked to 50 m extending into the ocean from shore (Figure 4.2; Figure A4.4). We then calculated meter-scale zonal statistics of live coral cover and water depth in each buffer and divided the median live coral cover by the mean water depth for each. (We used median live coral cover to avoid patches with particularly high or low coral cover overly skewing our data.) Next, we computed the change in depth-weighted live coral cover from 0 m to 50 m away from shore at each site (i.e., the linear model gradient of the five 1,000 m by 10 m buffers stacked at increasing distances from shore). We chose a scale of 0 to 50 m to encompass a range of visitation intensities at each site, as fewer on-reef visitors are likely to be 50 m away from land than right at and by the shore.

Calculating the depth-weighted change in live coral cover allows us to approximate a gradient of human use at each site (visitation pressures attenuate with distance from shore) and to subsequently identify potential impacts of visitation *per s*e on live coral cover within each site. This approach also allows for a better accounting of site-specific differences in coral cover, including unobserved water or benthic conditions; unidentified ecological interactions; and natural or anthropogenic features of the littoral environment, such as embayments and dredging.

Using change in live coral cover in lieu of absolute values of coral cover also accounts for simultaneous causality when live coral simultaneously attracts yet suffers from visitation. For instance, if visitors are attracted to higher quality reefs, but their presence subsequently

impacts the health of those reefs, this could lead to a self-perpetuating cycle of the highest quality sites being selectively damaged from visitation, and a weak relationship between absolute live coral cover and visitation at a site at any given point. In such instances, absolute comparisons of live coral cover might not capture the full effects of the coral-visitation relationship.

We limited this analysis to the 100 most-visited sites, as social media-based visitation data are generally more accurate at data-rich (popular) sites.[141] Further, the top 100 sites provided ample variation in visitation intensity across bays and beaches and mirrored the distribution of visitation intensities across all sites (Figure A4.5).[138,141] Through a visual inspection of histograms for on-reef and overall visitation at these 100 sites, we noticed a discontinuous distribution of visitation between the top 10 most-visited and bottom 90 less-visited sites (Figure A4.5). Based on this result, we split our sample size into the most- (top 10) and less-popular (bottom 90) sites and ran a non-parametric Mann Whitney U test to look for significant differences between these groups (Figure 4.2). While the discontinuous distributions shown in Figure A4.5 provide a compelling reason to split our dataset at the 10/90 cut-off, these results were also robust to different splits of the data (tested to a 40/60 split).

Controlling for depth provides a way to account for potential confounders that might affect both live coral cover and visitation rates with increasing distance from shore, as depth also strongly co-varies with temperature; light, nutrient, resource availability; and community composition.[170] While we could not control for these and other variables directly, the small difference in mean depth over 50 m from shore was much smaller than should allow for

meaningful differences in community structure (the average and maximum depths in each buffer were increasing functions of no more than 5 m apart from 0 to 50 m from shore).

Next, we repeated this same analysis between the most- and less-polluted sites across Hawaii, using data provided by the Ocean Tipping Points project.[159] We ranked all coastal sites by nearshore effluent load within a 1,000 m by 100 m buffer area (Figure A4.4), and subsetted the top 100 sites to include for analysis. We split these sites into the top 10 most-polluted and bottom 90 less-polluted sites, just like our visitation analysis, and ran a non-parametric Mann-Whitney U test between groups.

We also conducted a series of randomization inference procedures (placebo analyses) to test for model misspecification in our gradational analysis of coral cover change at and across sites of varying levels of visitation. We conducted two types of randomization procedures:

1. Using the most popular 100 sites obtained from our original gradational analysis, we randomly assigned visitation rankings to each site, which we subsequently split into two random sub-groups of 10 "most-visited" and 90 "less-visited" sites, identical to the methodology above. We conducted a non-parametric Mann-Whitney U test between groups and repeated this process across 10,000 runs in a Monte Carlo simulation. Aggregating these results, we calculated the proportion of runs that reported a significant result ($p \leq 0.05$), which came out to 4.58% for the top 100 overall sites and 5.05% for the top 100 on-reef sites.
2. We randomly assigned visitation rankings to all sites in our data ($n = 333$), 100 of which we randomly sub-sampled for our gradational analysis. We repeated the same

analysis with these 100 sites as above, and aggregating these results, we calculated the proportion of runs that reported a significant result ($p \leq 0.05$), which came out to be 5.12% for the top 100 overall visitation sites and 4.75% for the top 100 on-reef visitation sites.

Because the proportion of significant to non-significant runs of these placebo analyses (at the $p = 0.05$ level) was ~5%, we have confidence that the original observed visitation impacts on live coral cover change are not spurious. In other words, splitting the dataset into more- and less-popular sites is essential to finding a significant difference in live coral cover change, the results of which are unlikely to have arisen as an artifact of spurious correlations between variables (methods adapted from Hsiang and Jina, 2014).[171]

A4.3: Supplemental Figures and Tables

Figure A4.1: *Aggregated Instagram visitation data plotted against yearly daily censuses at the county level conducted by the Hawaii Tourism Authority from 2018 to 2021.*

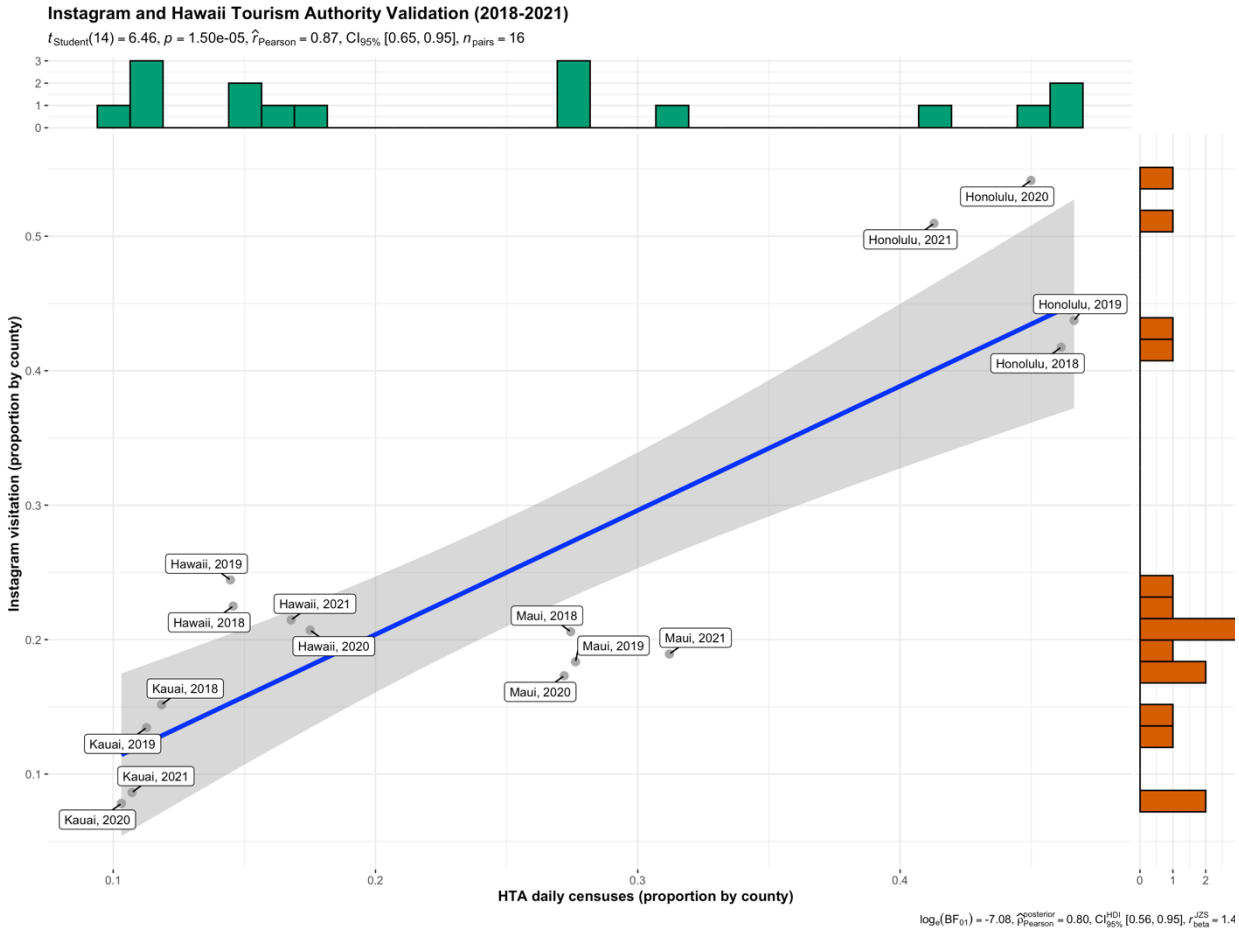

Figure A4.2: *Overall visitation at the top 20 most-visited overall sites plotted against absolute median live coral cover at each of these sites. The name, location, and rank of the top 10 most-visited sites are labeled.*

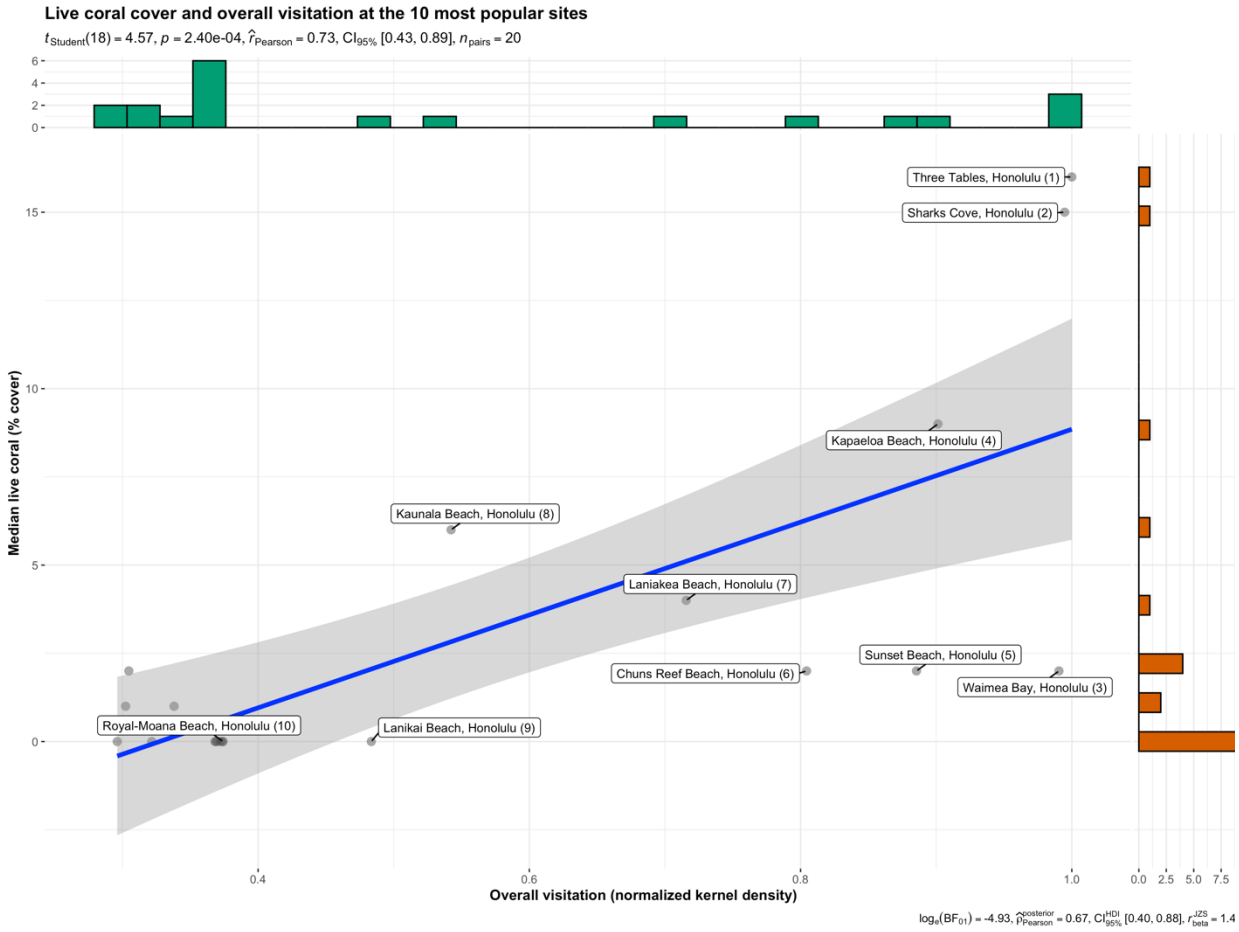

Figure A4.3: *The relationship between on-reef and overall visitation across 333 bays and beaches in the main Hawaiian islands (R^2 = 0.81).*

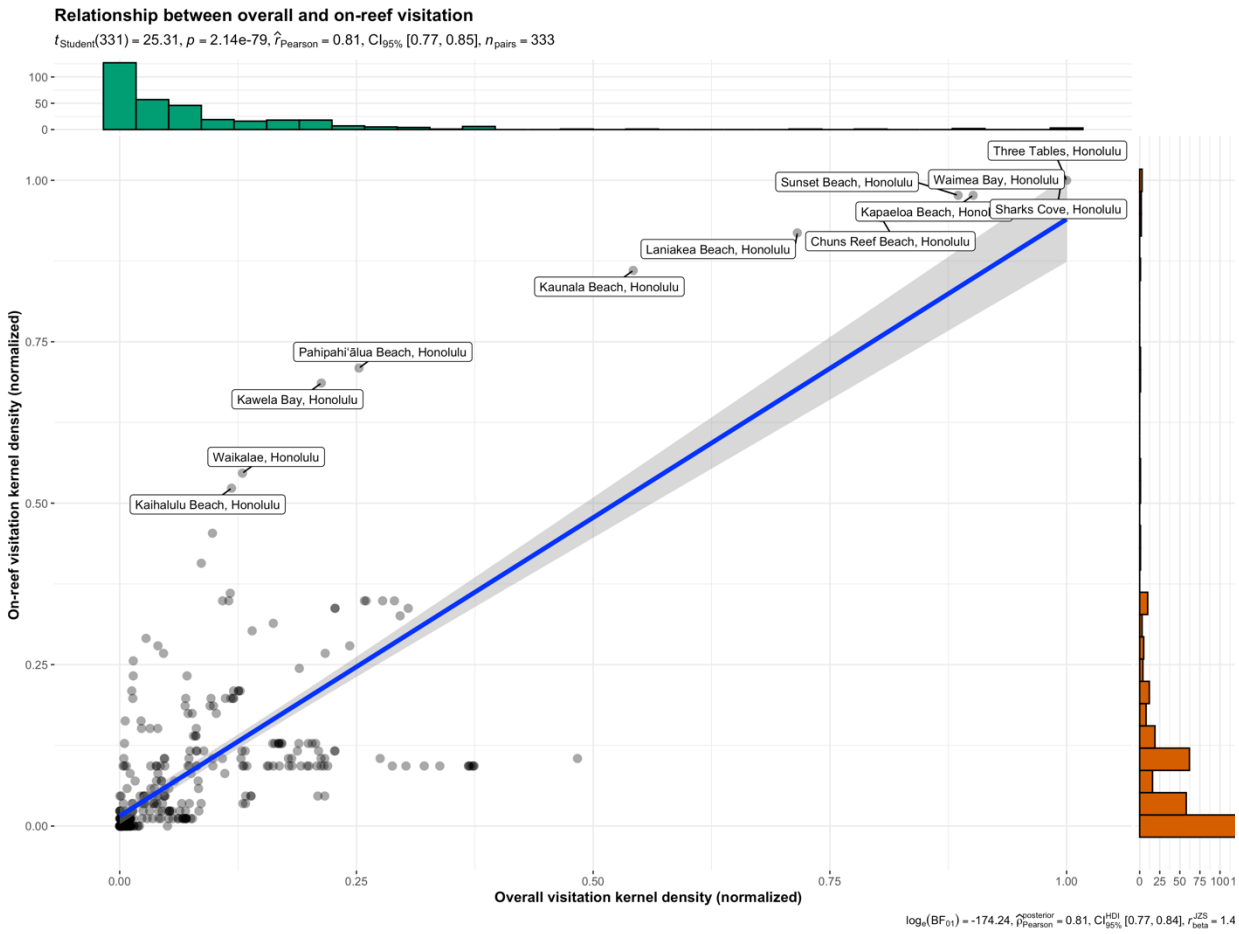

Figure A4.4: *A schematic of how each littoral buffer was constructed in ArcGIS Pro 3.0 for various calculations of benthic composition, human activity, and water condition at each coastal site.*

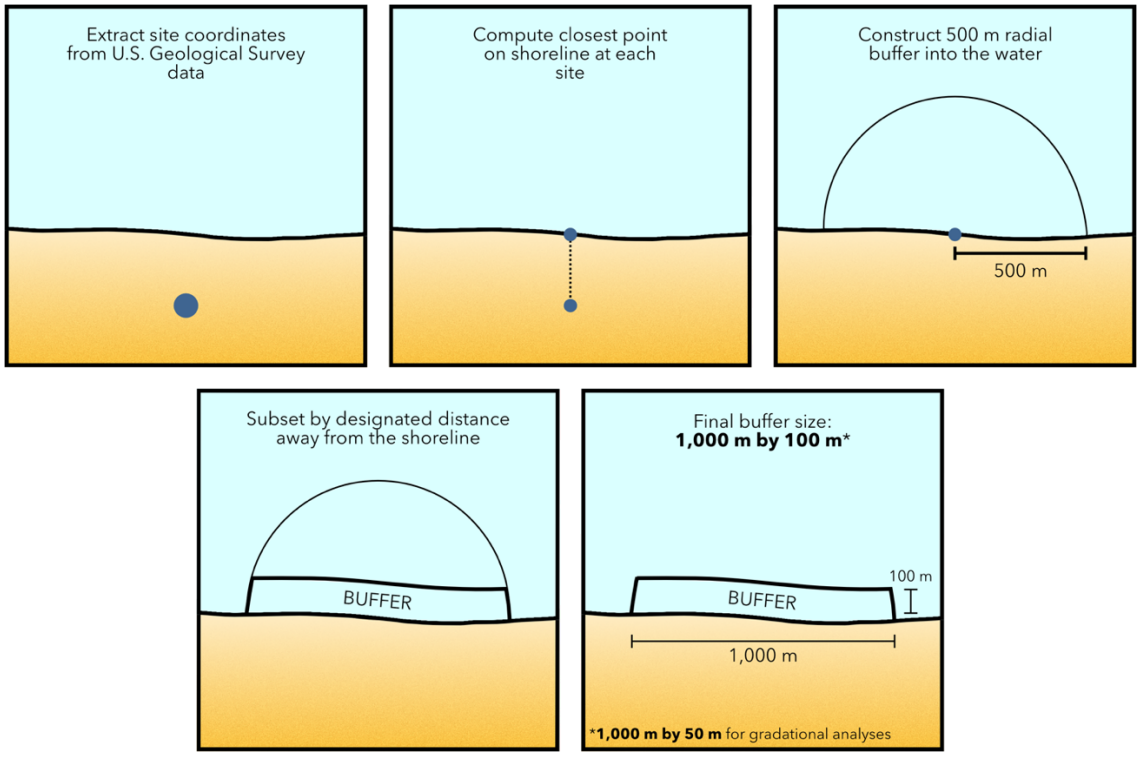

Figure A4.5: *Histograms showing a discontinuous distribution between high- and low-visitation sites for both overall visitation (top figures) and on-reef visitation (bottom figures) for most-visited sites (n = 100) and across all sites (n = 333).*

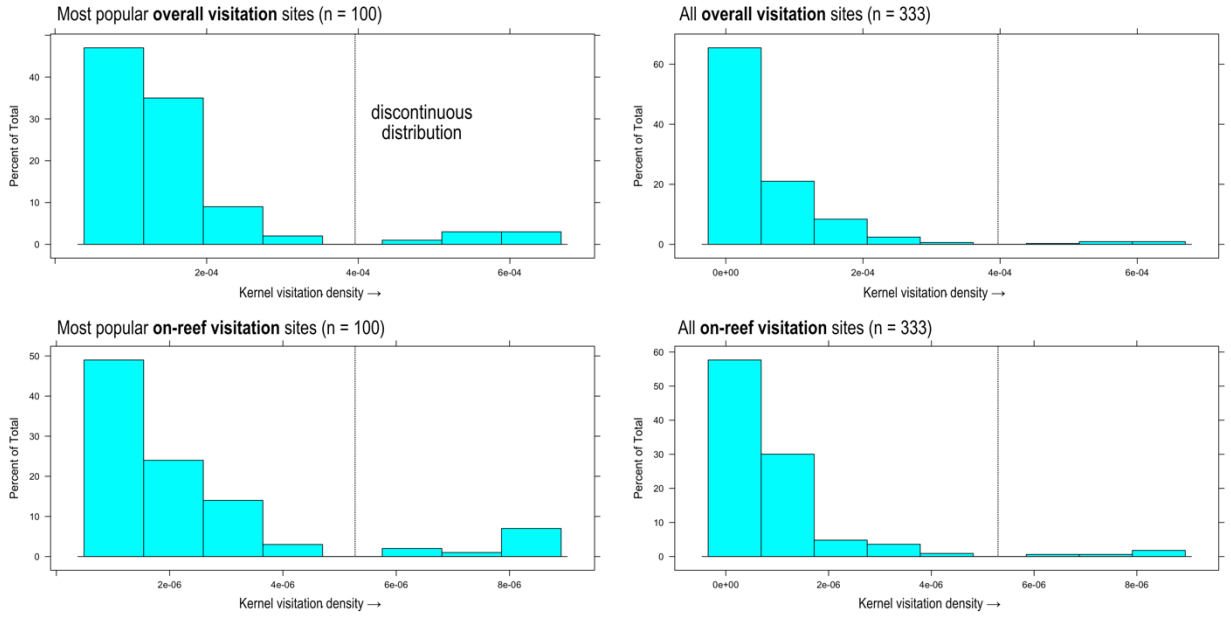

Table A4.2: *Most visited Hawaiian bays and beaches based on kernel visitation densities for both overall and on-reef visitation.*

Rank	Site Name	County	Site Location	Latitude	Longitude	Post Density (normalized)
Overall visitation						
1	Three Tables	Honolulu	Waimea	21.645761	-158.06393	1
2	Sharks Cove	Honolulu	Waimea	21.650388	-158.06321	0.99472296
3	Waimea Bay	Honolulu	Waimea	21.640994	-158.06601	0.99053236
4	Kapaeloa Beach	Honolulu	Waimea	21.628628	-158.0738	0.90128822
5	Sunset Beach	Honolulu	Waimea	21.664428	-158.05206	0.88545709
6	Chuns Reef Beach	Honolulu	Haleiwa	21.623521	-158.08112	0.80443893
7	Laniakea Beach	Honolulu	Haleiwa	21.619013	-158.08523	0.71566041
8	Kaunala Beach	Honolulu	Waimea	21.682215	-158.03256	0.54229396
9	Lanikai Beach	Honolulu	Mokapu Point	21.390141	-157.71342	0.48347043
10	Royal-Moana Beach	Honolulu	Honolulu	21.275348	-157.82562	0.37420456
11	Waikīkī Bay	Honolulu	Honolulu	21.274818	-157.82762	0.37373894
12	Waikīkī Beach	Honolulu	Honolulu	21.276608	-157.82865	0.37234208
13	Sans Souci Beach	Honolulu	Honolulu	21.26816	-157.82287	0.37001397
14	Grays Beach	Honolulu	Honolulu	21.277248	-157.83165	0.3686171
15	Kapiolani Park Beach	Honolulu	Honolulu	21.26731	-157.82265	0.36830669
16	Kaluahole Beach	Honolulu	Honolulu	21.257613	-157.81762	0.33804129
17	Magic Island Lagoon	Honolulu	Honolulu	21.282876	-157.84701	0.32158932
18	Ulua Beach	Maui	Makena	20.690587	-156.44379	0.30467174
19	Kuilei Beach	Honolulu	Honolulu	21.255747	-157.80447	0.30234363
20	Keawakapu Beach	Maui	Makena	20.70237	-156.44587	0.29613534
On-reef visitation						
1	Sharks Cove	Honolulu	Waimea	21.650388	-158.06321	1
2	Three Tables	Honolulu	Waimea	21.645761	-158.06393	1
3	Waimea Bay	Honolulu	Waimea	21.640994	-158.06601	1
4	Kapaeloa Beach	Honolulu	Waimea	21.628628	-158.0738	0.976744119
5	Sunset Beach	Honolulu	Waimea	21.664428	-158.05206	0.976744119
6	Chuns Reef Beach	Honolulu	Haleiwa	21.623521	-158.08112	0.94186047
7	Laniakea Beach	Honolulu	Haleiwa	21.619013	-158.08523	0.91860465
8	Kaunala Beach	Honolulu	Waimea	21.682215	-158.03256	0.86046512
9	Pahipahi‘ālua Beach	Honolulu	Kahuku	21.695873	-158.01625	0.70930233
10	Kawela Bay	Honolulu	Kahuku	21.69683	-158.01069	0.68604651
11	Waikalae	Honolulu	Kahuku	21.705483	-157.99679	0.54651163
12	Kaihalulu Beach	Honolulu	Kahuku	21.704486	-157.99138	0.52325581
13	Punapalaha	Honolulu	Kahuku	21.708842	-157.98497	0.45348837
14	Hanaka‘ilio Beach	Honolulu	Kahuku	21.709091	-157.97812	0.40697674
15	Kealakekua Bay	Hawaii	Honaunau	19.475089	-155.92857	0.36046512
16	Changs Beach	Maui	Makena	20.663204	-156.44156	0.34883721
17	Ke‘ei Beach	Hawaii	Honaunau	19.461805	-155.92478	0.34883721

18	Kapahukapu Manini Beach	Hawaii	Honaunau	19.471159	-155.92094	0.34883721
19	Palauea Beach	Maui	Makena	20.670613	-156.44282	0.34883721
20	Polo Beach	Maui	Makena	20.67587	-156.4435	0.3488372

Table A4.3: *All variables tested in the random forest models.*

GAO = Global Airborne Observatory; OTP = Ocean Tipping Points project; HSGISP = Hawaii Statewide GIS Program; SST = Sea surface temperature, LCC = Live coral cover.

Feature	Variable type	Description	Units	Source
LCC (sum)	Benthic composition	Sum of all LCC values at each site	Σ % cover	GAO
LCC (mean)	Benthic composition	Mean LCC at each site	% cover	GAO
LCC (median)	Benthic composition	Median LCC at each site	% cover	GAO
LCC (maximum)	Benthic composition	Highest LCC value at each site	% cover	GAO
LCC (range)	Benthic composition	Range of LCC at each site	% cover	GAO
LCC (majority)	Benthic composition	Mode LCC value at each site	% cover	GAO
Recreational fishing (shore)	Human activity	Non-commercial, shore-based fishing	kg ha^{-1} yr^{-1}	OTP
Recreational fishing (all)	Human activity	Non-commercial boat-/shore-based fishing	kg ha^{-1} yr^{-1}	OTP
Fishing (all)	Human activity	All shore-/boat-based fishing	kg ha^{-1} yr^{-1}	OTP
Nearshore effluent (all)	Water quality	Total effluent from sewage disposal	gal km^{-2} d^{-1}	OTP
Nearshore nitrogen	Water quality	Nitrogen flux from sewage disposal	gal km^{-2} d^{-1}	OTP
Nearshore phosphorous	Water quality	Phosphorous flux from sewage disposal	gal km^{-2} d^{-1}	OTP
Average SST	Water quality	Mean of weekly SST	°C	OTP
Average wave power	Water quality	Mean of maximum daily wave power	kW m^{-1}	OTP
Water depth	Water condition	Water depth data from 0 m to 16 m	% cover	GAO
Hotels weighted by units	Accessibility	Number of hotels weighted by available units	–	HSGISP
Number of hotels	Accessibility	Number of hotels across Hawaii	–	HSGISP
Nearest road distance	Accessibility	Distance to the closest road	m	HSGISP

Chapter 5 — Reforms and regulations for adaptive on-reef tourism management for the world's coral reefs

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Abstract

Intentional and unintentional physical contacts between scuba divers and the seabed are made by most divers and multiple times per dive, which often results in damage to corals and other marine life. Current efforts to reduce reef contacts (e.g., voluntary dive operator recognition programs and voluntary dive standards) can be effective, but lack sufficient incentive structures for long-term compliance. In their current capacity, these programs fail to reduce reef contacts to tolerable levels. Regulatory policies can facilitate pervasive and permanent shifts in human behavior, but have been underutilized to change unsustainable underwater norms. Most coral reefs open to recreational diving lie within territorial waters of individual countries, and many already have existing forms of protection with legislation that can be easily modified. Successful policy precedents in MPAs (e.g., bans on underwater glove-use) and elsewhere (e.g., anti-smoking laws in public spaces and legislation enforcing seat belt use) demonstrate the largely untapped potential of using effective governance to change destructive diving norms for good. To reduce intentional reef contacts, policy-makers can enact regulations in MPAs directly banning all contact between divers and the seabed. To reduce unintentional contacts, policy-makers can create policy safeguards that preempt such occurrences (e.g., requiring divers to

keep a certain distance from the seabed). Crucially, such policies will need accompanying formal and informal enforcement measures that are equitable, effective, and efficient to motivate compliance and effect lasting behavior change. Having a robust, well-enforced, regulatory framework to tackle both types of reef contacts is key to permanently changing divers' underwater attitudes and fostering sustainable scuba diving behavior to the benefit of all.

5.1: Diver-reef contacts in context

Coral reefs are inordinately important to marine biodiversity and humans,[172,173] yet are on a steep global decline.[174–176] Concurrently, recreational scuba diving has become a multi-billion-dollar industry,[177] with over a million new divers gaining certification each year.[178] Despite its non-extractive nature, recreational diving can still adversely affect reef ecosystems, both directly and indirectly. Direct effects involve intentional and inadvertent damage to corals and other marine life.[179–184] Indirect impacts associated with higher diving pressures include sediment deposition from fin kicks,[185] elevated rates of coral disease,[186] and shifts in ecosystem dominance and structure.[187]

Scuba divers can directly damage reef life through physical contact between any part of their bodies or diving equipment and the seabed; these are called reef contacts.[185] Reef contacts can be intentional, usually from reef-holding for support or out of apparent curiosity for handling and examining wildlife,[188] or unintentional, often from a lack of situational awareness, care, or underwater buoyancy control while diving.[189–192] Studies find that between 71 to 98 percent of all scuba divers make (intentional or unintentional) reef contact at least once every dive,[191,193] with an average reef contact rate for divers ranging from 0.2 to over 4.0 reef contacts

per minute of diving.[194,195] Of such contacts, over a quarter can cause visible damage to corals or other marine life.[189,190] Further, because reef contacts might also include impacts with non-living components of the seabed (e.g., dead coral or rubble), reef contacts directly involving live coral have even higher rates of damage (up to 74% of contact instances in one study; Krieger and Chadwick 2013), especially with respect to branching corals.[185,196]

High reef contact rates pervade even amongst divers with advanced certifications or high experience levels, putting reefs at risk of damaging contacts from divers of all levels of expertise.[188–190,197,198] Reef contacts also have widespread geographic documentation, including in Australia,[195,196] Hong Kong,[189] Israel,[185] Italy,[198] Japan,[191] Mexico,[134,184] the Philippines,[190] Spain,[199] St. Lucia,[197] Thailand,[192] and the United States.[188,193] When reef contacts and their associated damages to marine life are compounded across millions of divers every year, multiple times a dive, and all over the world, the cause for conservation concern becomes clear.

5.2: Existing efforts lack resolve

Several programs and initiatives have tried to reduce divers' reef contact rates, sometimes successfully and sometimes not. The most coordinated approach, voluntary dive operator recognition programs, involve granting individual dive centers "eco-certifications" when they choose to adhere to certain diving standards. "Green Fins", one of the largest of such initiatives, is an operator recognition program that requires its member dive centers to "promote a strict 'No Touch' policy for all reef diving and snorkeling."[200] Choosing to dive with "certified" dive centers can lead to significant reductions in reef contact rates.[188,190,193,201] However, in their current capacity, such programs lack sufficient incentive structures necessary for long-term compliance and remain largely localized. For example, while Green Fins may

have had over 600 dive-operator members across 11 countries since 2014, only 143 of these dive centers were still active in 2020, most of which are concentrated in Southeast Asia.[202]

A similar approach to reduce reef contacts is through voluntary dive standards. These diving guidelines are voluntary codes of conduct on how to reduce underwater environmental impacts, distributed by non-governmental organizations to conservation-minded divers and dive operators. The Coral Reef Alliance has a published list of voluntary standards for diving in the Mesoamerican Barrier Reef System, which informs divers to not "touch or contact corals or other reef dwelling organisms."[203] These guidelines are free for divers and dive operators to adopt, compliance is optional, and standards are often region specific. The Maui Reef Fund, a program initiated by the Hawai'i Wildlife Fund, has a different set of standards for diving in Hawaii. These standards ask that divers and dive leaders "not handle marine life except on rare occasions" and to "look before touching the bottom for balance, making sure it is non-living substrate."[204] When different organizations promulgate inconsistent, non-binding standards across geographic regions, it can be difficult for divers to deviate from the prevailing status quo of high reef contact rates.

Specific approaches to reducing reef contacts recommended by many existing initiatives involve the use of instructional dive briefings and direct underwater interventions to discourage reef contacts. Pre- and post-dive briefings admonishing divers to reduce reef contacts range from having little to large success on reducing real-world contact rates,[194,197] suggesting that the quality of instruction may be an important mediating variable.[188] In-water interventions involve dive-leaders immediately bringing to attention any observed reef contacts made by divers in

their dive group. These can significantly reduce reef contacts,[197] but may be undermined when dive professionals themselves frequently make reef contact.[190]

The persistent rampancy of reef contacts suggests that, in isolation, voluntary approaches may not be adequate to properly address the reef contact problem. The prevalence of both intentional and unintentional contacts may be symptomatic of a diving culture that perceives reef contacts to be less of a conservation problem than they really are. If reef contacts are viewed as a small and inevitable side effect of diving, this likely propagates unsustainable expectations of what scuba diving entails, and facilitates underwater social norms that subsequently excuse their occurrences. As such, viable long-term solutions will need to change the underlying structure of divers' attitudes towards reef contacts in order to better incentivize systemic, long-term compliance.

5.3: Harnessing policy change for norm change

The introduction of regulatory policies to reduce reef contacts can have positive, knock-on effects in facilitating an underwater social norm change. Social norms have varying definitions across disciplines, but generally comprise a constellation of predominant behaviors and attitudes towards what is acceptable within a group.[205] Since human behaviors are often driven by conformity to other's expectations and behaviors, policies provide opportunities for people to change their beliefs towards what is considered acceptable behavior.[206] Once behavioral expectations are established, the share of norm-followers increases in tandem with the strength of social sanctions against norm-violators, and a self-reinforcing cycle of virtuous behavior change can ensue.[207]

For example, following amendments to Norway's anti-smoking laws in 1988, the country saw widespread changes in attitudes towards smoking. While the law itself only prohibited smoking in certain public places (e.g., work premises and public transport), Norway saw wide-reaching effects on smoking norms even outside of the law's purview. Today, smoking in Norway almost never occurs indoors, including in previously unregulated spaces (e.g., private homes). This occurred despite limited governmental enforcement, driven predominantly by stricter social sanctions from non-smokers towards smokers. As anti-smoking laws led to less exposure to smoking in the general public, societal tolerance towards acts of public smoking also decreased, leading to even higher social sanctions and even less public smoking.[208] Similar examples of policy-driven social norm shifts include the prevalence of seat belt use following enforcement legislation in North America,[209,210] the abrupt end to female foot-binding in China,[211] and the successful uniform invoice lottery system to combat tax evasion in Taiwan.[212]

The use of similar legislation to regulate reef contacts may help alter unsustainable underwater norms. Policies are especially poised to create tipping points of behavior change when adopting the behavior in question is (1) easily observable, (2) enjoys coordination benefits (a behavior is more readily practiced as it becomes more widespread), and (3) faces low compliance costs.[207] Reef contacts (and their absence) are highly observable, as recreational diving is never done alone, and even unintentional or unnoticed contacts are equally visible to others. Coordination benefits also exist as reef contacts become less frequent. Recreational diving is done in buddy pairs, and divers are taught to always keep near to and at uniform depth with their dive buddies or dive group. Thus, divers maintaining a safe distance from the

reef also impact their partners' behaviors, making stray reef contacts less likely for all. Further, as most divers care deeply about the world's coral reefs,[188] social sanctions against reef contacts should rise as reef contacts become rarer, making divers less and less likely to make intentional contacts on a whim. Finally, foregoing reef contacts should also have relatively low compliance costs, since they are a by-product of diving and are by no means central to the sport's enjoyment (in fact, reef contacts can be extremely painful, and contact with benthic marine life can even be deadly).

5.4: Leveraging marine protected area legislation

Virtually all of the world's coral reefs open to recreational diving lie in territorial waters, within the exclusive economic zones (EEZs) of sovereign nations.[213] This means that individual governments decide how best to handle coral reef tourism in their countries' respective EEZs. In line with existing marine conservation agendas, many countries choose to establish marine protected areas (MPAs) in their coastal waters that limit, to varying extents, the extraction, consumption, and use of reef resources. These MPAs are negotiated on a case-by-case basis, are often updated, and include regulations and allowances for recreational diving.

The existing legislative framework of MPAs provides policy-makers the opportunity to integrate additional reef-protecting policies into MPA legislation with relative ease and without the need for international treaties or extra-national oversight. Such policies can be tailored to independently address both intentional and unintentional reef contacts, serving the dual purpose of directly reducing reef contacts in the places where they are in effect, and changing underwater norms that can impact divers' behaviors even in the places where such policies are not yet in effect. The value of coral reefs to tourists is also closely aligned to its perceived

ecosystem pristineness.[198,214] Many divers also care about reef conservation, are aware that their underwater actions do damage to reefs, and even prefer more restrictive regulatory management than the current status quo.[215,216] This suggests that effective and equitable policies to reduce damaging reef contacts also benefit economic returns on tourism revenue and should be in the interest of both policy-makers and divers to pursue.

5.5: Reducing intentional reef contacts

MPA policies are especially well-poised to reduce intentional reef contacts. By designating parts or all of MPAs open to recreational diving as "no-touch" zones, regulations can directly prohibit divers from making reef contacts at these sites. Observed and documented infractions would be open to formal sanctions (e.g., fines, permit suspensions, bans from subsequent visits, etc.), as imposed by marine park authorities.[184] At face value, formal sanctions may defy enforcement, given the opacity of underwater behaviors to regulatory scrutiny and the often-limited resources of marine park authorities. However, social sanctioning can play a pivotal role in achieving desired behaviors, even in light of limited formal enforcement.[208] A legislative ban on reef contacts formally flags such behaviors as "wrong", and encourages divers to self-police and subsequently course-correct their behavior to avoid social sanctions from dive peers and professionals associated with rule-breaking behavior. As reef contacts decrease in frequency, the perceived severity of subsequent contact events increases, leading to higher social sanctions and even fewer reef contacts. A "no-touch" policy may also incentivize divers to proactively correct for reef damages from unintentional collisions. Such measures might include diving a safe distance from the seabed, practicing proper buoyancy

control, streamlining scuba equipment, and avoiding dives in difficult areas or under rough conditions.

5.6: Reducing unintentional contacts

Many unintentional contacts occur with trailing scuba equipment, like diving fins, and can occur entirely unnoticed by divers. A "no-touch" policy may not be entirely effective to guard against such occurrences, as it is difficult to regulate behaviors that occur outside of a diver's awareness or ability to control. To forestall unintentional contacts, the use of policy safeguards may be more effective. This could be an MPA regulation requiring divers to maintain a certain distance from the reef at all times, thereby creating a "safety bubble" above the reef to preempt lapses in buoyancy control or situational awareness that may otherwise result in accidental reef contact. However, such a safeguard policy may also increase compliance costs, especially for specialist divers. Underwater photographers, for instance, may need to sacrifice a certain level of intimacy with underwater subjects in order to comply with such rules. However, camera-carrying divers consistently make more reef contacts than non-camera divers,[189,190,193,195,197,199] while also valuing intact reefs more than do generalist divers.[217] This suggests that fair, well-implemented policy safeguards should be in the interest of all types of divers to enact, and can lead to a better diving experience for all.

Other policy safeguards to reduce reef contacts may include stipulations on how large diving groups can be, what underwater conditions are permissible to dive under, and which types of finning techniques may or may not be used. Codes of conduct common in voluntary programs should also be better integrated into MPA regulations. These can include mandatory

pre- and post-dive briefings admonishing divers to reduce reef contacts, and additional buoyancy control and environmental awareness training in order to dive at certain sites.

5.7: Policy precedents

A handful of MPAs already have similar policies in place. In the Cabo Pulmo National Park in Baja California Sur, Mexico, divers are prohibited from swimming closer than 2.5 meters to the reef.[218] For the most part, this policy has been well-communicated, strictly enforced, and largely effective. In the last few decades, the park has also seen a concurrent revival of its fish biomass – the largest ecosystem recovery of any marine reserve.[219] Similarly, in Egypt, "touching corals and marine life is strictly prohibited" by the Egyptian Chamber of Diving and Water Sports, though the extent to which this policy is communicated to divers and diver operators remains uncertain.[220] Analogously, in Taiwan, the touching of marine wildlife (e.g., sea turtles) is strictly prohibited, and is periodically enforced under the country's Wildlife Conservation Act, though such regulations do not yet extend to cover reef contacts.[221] While promising, such policies remain noteworthy exceptions to the largely missed opportunity of harnessing regulatory action to minimize diver-reef interactions in MPAs.

A more prevalent policy precedent has been the (successful) prohibition on glove use while diving in many tropical MPAs (e.g., Surin Islands Marine National Park, Thailand; Sharm El Sheikh, Egypt; and Cozumel Reefs National Park, Mexico). This supposedly discourages indiscriminate reef-touching by removing material protection from incidental abrasions, cuts, spines, or stings that might occur through reef-handling. In MPAs with such regulations, only extenuating medical circumstances, like a proneness to hypothermia or open wounds, serve as a viable reason for glove-wearing.[222] Today, numerous divers dive without

gloves, even in tropical regions where glove-use is not prohibited. Other common conservation-oriented policy precedents include stipulations for mooring line use in lieu of dive boats individually throwing anchor,[182,223] and bans on dive knives or muck sticks in many MPAs.[218,220] Widespread compliance to these policies opens the door to more sweeping efforts to directly target reef contacts and better protect reefs from divers.

5.8: Looking forward

Reef-protecting policies are not a panacea to the reef contact problem. Formal enforcement will not be easy to implement, given limited resources of marine park authorities, and compliance will need to be largely driven by informal, social sanctions from within the dive community, plus the occasional prosecution. However, this has worked for other MPA policies (e.g., bans on glove-use) and in other domains (e.g., the success of many public anti-smoking laws), suggesting that social sanctions following policy changes can drastically alter human behavior, even with limited formal enforcement.[208] Such policies should supplement, not supplant, existing conservation regulations and initiatives, and existing, provenly-effective voluntary solutions should be expanded wherever possible. Indeed, such programs, like Green Fins, also work with local governments to strengthen national and regional regulations, laws, and policies, so their expansion could lead to beneficial outcomes in more than one domain.

Some sites may also benefit more from certain reef-protecting policies than others. For tourist hotspots of high conservation value or reefs particularly prone or sensitive to diver contacts (e.g., shallow reefs with many branching corals), for instance, a "safety bubble" approach mandating divers to keep a certain distance from the reef may be the best policy option. Such sites have much to gain from fewer damaging contacts, and relatively little to fear

from compliance costs driving divers away. Other sites may not be tenable for "no-touch" policies at all, like sandy-bottom areas used for dive-certification training, or areas with heavy currents that require close reef-swimming or even reef hooks. Regulatory tools will need to be thoughtfully tailored to the situations and sites that will benefit most from their implementation, all while making sure to keep stakeholders adequately informed, involved, and onboard.

In short, regulatory bans on reef contacts or safeguard policies to a similar effect remain an underutilized tool to changing destructive diving norms and should be adopted wherever feasible. Voluntary approaches have been tried and tested, yet they have not reduced damages from diver-reef contacts to a tolerable level. Perhaps it is time that top-down governance plays a more forceful role in facilitating behavior change. At the least, such policies can sustain and lend credibility to the admonishments of operator recognition programs, voluntary standards, scuba professionals, and diving peers to practice sustainable underwater behavior. At the most, affording coral reefs the additional protection of regulatory action can be the bold, yet pragmatic solution needed to permanently shift underwater norms for good.

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Chapter 6 — Key drivers of unsustainable tourist behaviors on tropical coral reefs

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Abstract

Coral reefs are vastly biodiverse and widely visited. Integrating new primary observational and questionnaire data, we find on-reef tourists in Southeast Asia systematically underestimate their harmful reef impacts and overestimate their underwater diving abilities. Observed coral contacts were largely unintentional or unnoticed damages (UUD) and closely associated with other tourists' behaviors, wildlife sightings, tour operator eco-certification, and accessory use. Adaptive, proactive, and socio-ecologically integrated conservation management is key for sustainable reef use.

6.1: Main Text

Coral reefs support a quarter of all marine life and provide invaluable ecosystem services, but are suffering a swift global decline.[9,10,12] Meanwhile, marine tourism is increasingly lauded as a promising pathway for sustainable reef use, comprises the largest sector of the $2.5 trillion global ocean economy, and features heavily in conservation and sustainability agendas.[224,225]

While reef tourism stands to benefit both the economy and the environment, its implementation and practical implications are often less salubrious. Through both direct (e.g., physical damage) and indirect (e.g., pollution, disease, and coastal development) stressors, tourism is a primary contributor to localized yet globally-occurring reef damages and exacerbates the effects of climate change on the world's reef ecosystems.[226,227]

Coral reefs in Southeast Asia are particularly at risk. The region's reef ecosystems are the world's most biodiverse, and its reef tourism is among the world's most popular yet understudied.[144,228] In this study, we collect novel primary observational and questionnaire survey data from 730 scuba-diving on-reef tourists across five reef visitation hotspots in the Philippines and Indonesia (Figure 6.1) (see Appendix for site inclusion criteria and sample representativeness [Table A6.1]). We observe tourists' behavior underwater, measure their attitudes and behaviors, and assess individual- and group-level factors associated with

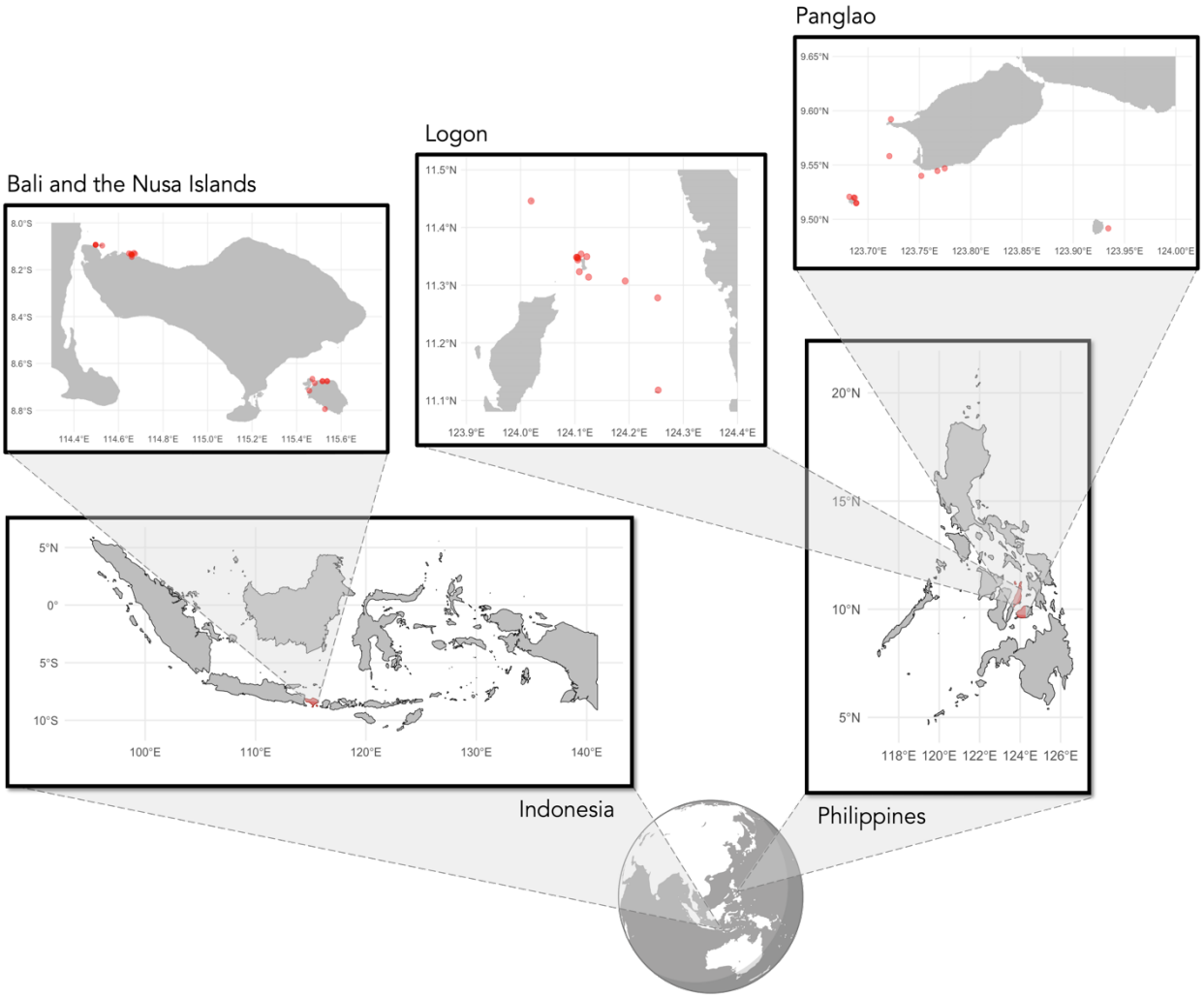


Figure 6.1: Map of reef visitation hotspots and observational study sites across Indonesia and the Philippines

unsustainable human-reef and human-wildlife interactions, which we complement with a rich qualitative survey of diving tourists' perceptions of their own and others' underwater behaviors (see Methods and Appendix).

Over 20,419 minutes of observation, we find consistently high levels of reef contacts and damages by on-reef tourists (1.96 ± 4.30 [mean ± SD] seconds of reef contact per minute of diving, 41.3% of which were reef damaging; n = 411 tourists) (see Appendix [Table A6.4]).

Such unsustainable behaviors contradict strong stated pro-environmental, reef-related attitudes and social norms across survey respondents (composite environmental score of 7.05 ± 0.68 [mean ± SD] out of 8.00) (see Methods and Appendix [Figure A6.3]). We also differentiate between intentional and accidental reef contacts, given important differences in their underlying causal mechanisms (see Methods and Appendix). Crucially, we identify unintentional and/or unnoticed damages (UUD) as a primary driver of tourists' reef-damaging behaviors (61.0% of all contacts were deemed as "accidental" and 53.3% as "unaware").

Across the board, on-reef tourists systematically *overestimate* their diving abilities and *underestimate* their reef impacts, even after controlling for potential sampling bias in our dataset. At least 69.0% and 85.7% of survey respondents consider themselves "above average" in their ability to avoid intentional and unintentional reef contacts, respectively, and 73.0% consider themselves at least "above average" in their ability to maintain underwater buoyancy control (see Appendix [Figures A6.4–A6.6]). As such perceptions statistically cannot reflect reality, our results affirm the "illusory superiority" effect in a new context.[229]

Further, using matched observational and questionnaire data, we report an attitude-behavior gap between respondents' perceived and observed reef impacts. Divers vastly underestimate (by 4.92 ± 0.926 [mean ± bootstrapped SE] times) the number of reef contacts they thought they made relative to how many contacts they were actually observed to make ($t(82.9) = -4.52$, $p < 0.001$ (see Appendix [Figure A6.7]).[230] On any given reef outing, observed reef contact rates are practically uncorrelated with subsequently self-reported contact rates, though subjects are generally better at predicting the number of intentional (versus accidental) contacts they made. Specifically, we also find that the worst-behaving divers are the

most overconfident in their underwater abilities. This is a striking example of the "Dunning-Kruger" effect, a cognitive bias whereby people with limited competence in a given domain are especially prone to overestimating their abilities (see Appendix [Figure A6.8]).[231]

Next, we use random forest machine learning models to unravel the associations behind reef contacts and various diver and dive features (Figure 6.2). Random forest models were chosen for their robustness to skewed and non-linear datasets while retaining high accuracy and efficiency (CITE). Overall, we find that reef contacts are most closely associated with: (1) the contemporaneous behaviors (i.e., contact rates) of co-recreating guests and guides; (2) wildlife sightings; (3) tour operator eco-certification; and (4) underwater accessory use (i.e., camera, glove, and muck stick).

Our finding (1) that the behaviors of on-reef tourists closely relate to those of their co-recreating peers and leaders has clear conservation and behavioral implications. Descriptive social norms refer to the perceived prevalence of behaviors that others are doing, while injunctive social norms refer to the perceived prevalence of behaviors that others ought to be doing.[232] In social contexts where conformity and imitation are prevalent, unsustainable reef contacts, as a descriptive social norm, are likely reinforced. However, on-reef tourists also exhibit strong injunctive social norms towards reef and marine conservation (see composite environmental scores). Consequently, such conditions provide a novel opportunity to catalyze virtuous cycles of behavior change (see intervention recommendations below).

Our unique dataset also allows for (2) a novel causal analysis of wildlife sightings on reef contact probability (see Appendix for causal inference analyses). We find that underwater wildlife sightings cause tourists to increase their intentional, unintentional, and damaging reef

contacts (by 220%, 85%, and 106% respectively). Such behaviors represent a new type of tourism paradox: wildlife observations, the underlying reason why many reef tourists choose to recreate, directly contribute to the subsequent degradation of the reef habitats upon which such wildlife depend. This finding is critical for reef management, and lends additional credence to reef-protecting policies at sites of special wildlife renown, especially when such sites are also subject to high tourist loads.

A deeper dive into (3) tour operator eco-certification schemes reveals nuance in their ability to mitigate reef damages. Green Fins, the world's largest dive operator eco-certification program, certifies on-reef tour operators that adhere to its above- and below-water codes of conduct for sustainability best practices.[200] In our data, Green Fins certification does not correlate with reductions in total (accidental plus intentional) reef impacts, contrary to previous findings [233]. However, Green Fins certification *is* significantly associated with reductions in *intentional* reef contacts, especially for dive guides and at the highest ratings of eco-certification (i.e., Gold-rated operators) (Figure 6.2). As Green Fins–certified operators do not choose their guests, it is encouraging that eco-certification is associated with more sustainable guide behaviors, and reinforces its potential to facilitate trickle-down pro-conservation behaviors in reef-visiting guests.[234] Importantly, however, eco-certification schemes are not a panacea for reef damages in isolation, and should be supplemented with additional reef-protecting policies and adaptive conservation management.

Finally, the association (4) between on-reef accessory use and reef contacts and damages has been well replicated in the literature (Figure 6.2).[234–237] To limit the adverse impacts of often-unnecessary underwater accessories, effective tourism management could

prohibit, limit, or tax their use. Less intrusive interventions could involve publicizing their known negative consequences to reef guides and guests, both to encourage responsible recreation as well as to elicit informal social sanctions against associated reef-damaging behaviors.

Our findings support additional conservation measures. Behavioral interventions (e.g., through policy change) have the potential to trigger knock-on effects in a positive feedback loop [238]. Interventions that improve the behaviors of social referents (e.g., dive guides) and the worst-performing on-reef tourists can thus produce knock-on conservation outcomes, both to curb immediate reef-damaging behaviors as well as to create the conditions necessary to facilitate a social tipping point towards a positive, self-reinforcing social norm. This could be achieved through refinements to the recreational and professional dive certification process by international certification agencies (i.e., raising the standards of reef conservation awareness and technical training necessary for certification). Reef-protecting legislation, implemented and enforced at the federal or marine protected area levels, can also directly decree pro-environmental behaviors (e.g., Indonesia's reef tourism regulations).[239]

Further, given the prevalence of unnoticed and unintentional reef damages (UUD), decision-makers could also directly implement structural and proactive reef damage mitigation (e.g., a "safety bubble" policy approach prohibiting all close reef swimming).[133] Stronger interventions that publicize the under-appreciated prevalence of tourist-reef impacts could also be directed towards divers, both correctively (e.g., in-water guidance) and preemptively (e.g., pre-dive briefings and variable guide–guest ratios based on customer experience levels). Informational campaigns could further underscore pernicious tourist-reef damages, including

the use of descriptive and injunctive social norm messaging disseminated via dive briefings, in dive shops, and through the dive certification and dive operator eco-certification process.[197,236,240]

Our results suggest that reef stakeholders must better integrate the hidden consequences of reef tourism on underwater natural environments and wildlife in current and future tourism-as-revenue calculations. By and large, on-reef tourists are firm proponents of reef conservation, and most reef impacts are unintentional and go unnoticed (UUD). Therefore, any comprehensive conservation management plan should account for such types of reef degradation. Special attention should also be paid to the downstream detrimental effects that reef damages can have on the economy at various scales. Degraded reefs are not only less attractive to tourists, jeopardizing opportunities for tourism monetization, but are also less able to provide other ecosystem services (e.g., provisioning fish stocks).[241,242] Ultimately, only by understanding the socio-ecological conditions underlying unsustainable underwater behaviors can the right interventions be designed to foster sustainable human-reef interactions to the betterment of both local economies and reef ecosystems everywhere.

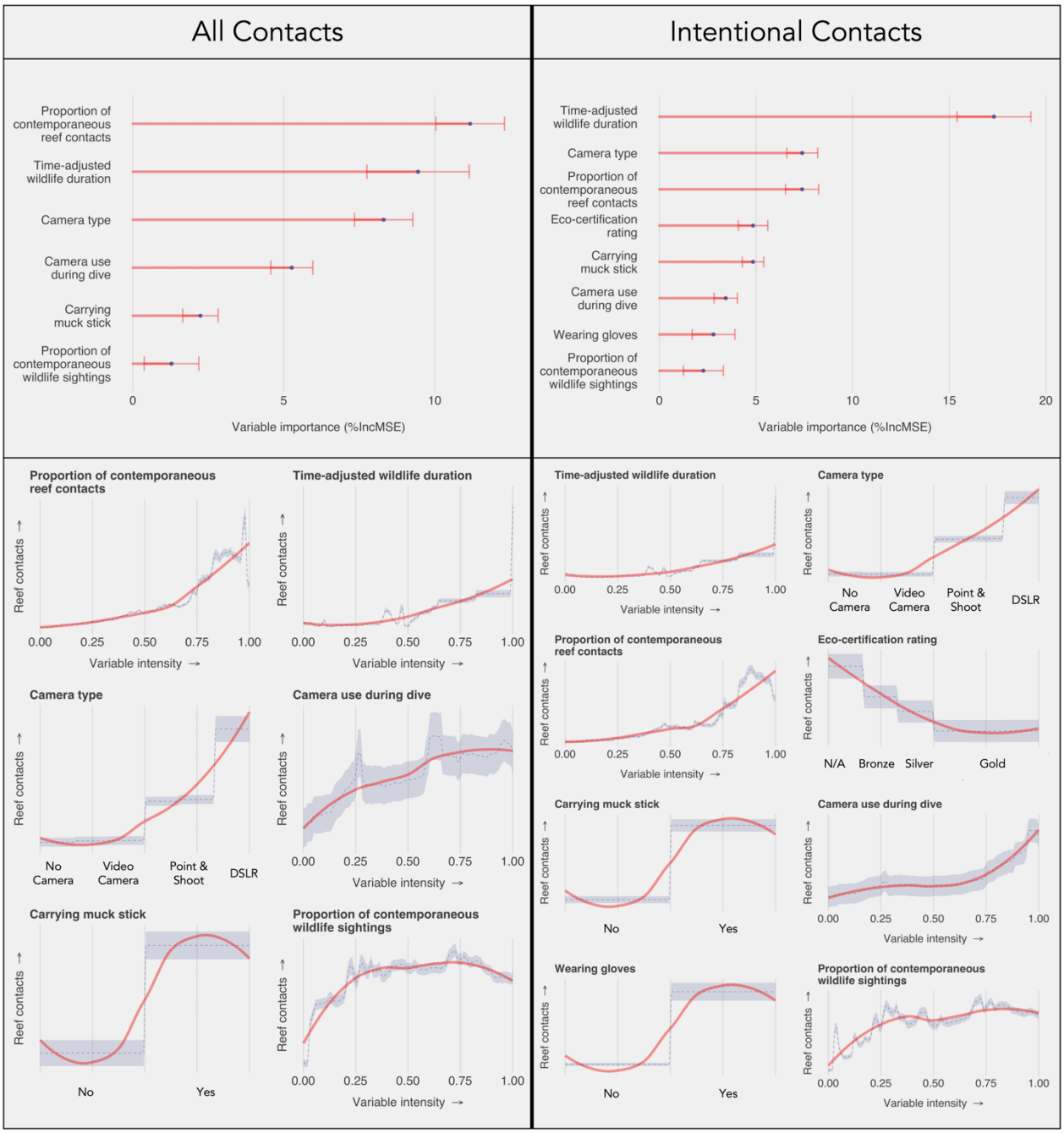


Figure 6.2: Variable importance and partial dependence plots from random forest machine learning models for total reef contacts (R^2 = 0.325 ± 0.121; r.m.s.e. = 0.0981 ± 0.0235) and intentional reef contacts (R^2 = 0.362 ± 0.118; r.m.s.e. = 0.0776 ± 0.0193) made by on-reef tourists (mean ± SD).

6.2: Methods

From December 2022 to January 2024, we collected behavioral and questionnaire survey data on a total of 730 on-reef tourists in Southeast Asia regarding their perceived and actual reef impacts (see Figure 6.1 and Appendix [Figures A6.1–A6.2]). In collaboration with 36 scuba diving operators in Indonesia (Bali and the Nusa Islands) and the Philippines (Logon, Dauin, and Panglao), we conducted a video-assisted underwater visual census of scuba diving on-reef tourists to assess the relative contributions of individual- and group-level factors associated with unsustainable reef-related behaviors. Subjects were informed of an ongoing reef conservation study but were not given additional details to minimize observer bias.

For each on-reef tourist observed on each research dive, we manually transcribed the type, timing, and duration of all reef contacts and wildlife sightings made, along with 22 concurrent dive (e.g., current strength, reef geomorphology, etc.), diver (e.g., camera/glove/muck stick use, contact intentionality, reef damage severity, etc.) and dive operator variables (e.g., eco-certification rating, pre-dive environmental briefing, etc.) from our video data ex-post (Table A6.3). We created a unique diver-second dataset comprised of every observed second of each observed diver, totaling 1,225,132 observations, and collapsed it to both the minute- and diver-level for subsequent analyses (see Appendix).

We used random forest machine learning models to assess the relative contributions of dive-, diver-, and dive operator-related variables to various types of on-reef contacts (Figure 6.2). Random forest regressions were chosen for their robustness to non-linear feature relationships and missing or outlier data common to socio-ecological systems, including in a variety of reef-related contexts.[243,244] We calculated each feature's average variable inflation

factor, mean decrease accuracy (%IncMSE), and bootstrapped 95% confidence intervals for partial dependence plots over 100 runs, and compared each model's R^2 and r.m.s.e. between training and testing datasets (Figure 6.2).

Questionnaire surveys were administered through Qualtrics via an online QR code that was disseminated through placards both placed at participating dive shops and handed directly to subjects who had been filmed while diving. The questionnaire was broken down into four sections: "Dive and Diver Information", "Perceived Underwater Impacts and Abilities", "Pro-Environmental Attitudes", and "Additional Background Information". It also included questions on whether respondents were accompanied by a researcher during their dive for matched observational analyses (see Appendix).

To assess tourists' perceptions of their underwater environmental impacts and abilities, survey questions asked subjects to rank their perceived abilities and reef impacts relative to those of other divers (e.g., "below average", "average", and "above average"). We created a composite environmental score, out of a total possible score of 8.00, for each survey respondent based on their feelings of compulsion and embarrassment towards performing (and being seen performing) various reef-related behaviors (see Appendix).[217] All study protocols were conducted in accordance with the approved guidelines of the Institutional Review Board (IRB) at Princeton University.

Acknowledgements

We thank all the dive shops that participated in this study across Logon, Philippines (Devocean Divers, Evolution Beach & Dive Resort, Fun'N'Sun Malapascua, Kokay's Diving Shop, and MTD Dive Shop); Dauin, Philippines (AivyMaes Divers, Aldive Resort, Aqua

Ventura Divers, Bongo Bongo Divers, Liquid Dumaguete, and Silver Reef Dive Resort); Panglao, Philippines (Blue Revival Diving College, Philippine Fun Divers, Piratas Alona Dive Center, Seaquest Dive Center, Sierra Madre Divers, and Valm Divers,); Bali, Indonesia (Abyss Ocean World, Dive Concepts Pemuteran, Easy Divers, Karang Divers Bali, and Mydas Dive Center); Nusa Lembongan, Indonesia (Big Fish Diving, Dive Concepts Lembongan, French Kiss Divers Lembongan, Legend Diving Lembongan, Tamarind Divers, and World Diving Lembongan); Nusa Ceningan, Indonesia (Ceningan Divers); and Nusa Penida, Indonesia (DPM Diving Penida, Dune Penida Dive Shop, Legend Diving Penida, Mambo Dive Resort, Purple Dive Nusa Penida, and Sanctum Dive). We also extend special thanks to M. and A. Reed at Evolution Beach & Dive Resort; M. Nielsen at Bongo Bongo Divers; G. Cranenburgh at Mydas Dive Center; N. Holohan at Valm Divers; J. Teo and P. Whitehead at Blue Revival Diving College; G. Sukayadnya at Tamarind Divers; S. Zhang and D. Fang at Marelux; K. Kollwitz at Ultralight Camera Solutions; and M. Burghardt, E. Yoo, and B. White at Princeton University for project support. We are grateful to the Indonesian Research and Innovation Agency (BRIN) for providing ethical clearance (415/KE.01/SK/06/2023) and permitting (363/SIP/IV/FR/6/2023) in Indonesia, and to Hons. G. Truita, L. Dãno, and E. Arcay for research approval across localities in the Philippines. This material is based upon work supported by Princeton University, the High Meadows Foundation, the High Meadows Environmental Institute at Princeton University through the Mary and Randall Hack '69 Research Fund, and the Princeton Institute for International and Regional Studies.

Appendix

A6.1: Extended Introduction

A6.1.1: Motivation

Coral reefs contribute greatly to marine biodiversity, ecological functioning, and myriad ecosystem services. For global conservation agendas to prioritize effective, equitable, and enduring marine management, they must also foster and facilitate sustainable forms of coral reef use. One promising pathway to a sustainable blue economy is through tourism, which ostensibly benefits both the environment and the economy, and features heavily in the UN 2030 Agenda for Sustainable Development Goals.[131,245]

Recreational scuba diving and snorkeling is an especially fast-growing and prominent form of reef tourism, comprising a multi-billion-dollar industry spanning most coastal waters.[246] Each year, millions of diving tourists support hundreds of thousands of jobs by visiting coral reef sites all over the world, helping to make marine tourism the largest sector of the global ocean economy.[224] In practice, however, reef tourism is associated with a host of direct and indirect damages to reef environments and frequently fails to deliver on the promise of sustainable reef use.[133,247–249]

While direct reef damages from tourists might appear small in isolation, in aggregate, they are an unambiguous cause for conservation concern. Individual contacts are compounded across millions of divers every year, multiple times each dive, and over the world's most biodiverse and sought after reefs. Such visitation damages have been systematically detectable across hundreds of reef sites across an entire archipelago, presenting a pernicious problem for reef conservation and exacerbating local effects of climate change.[226,227]

A variety of studies have documented the negative impacts of on-reef tourist visitation, namely snorkeling and scuba diving, on reef ecosystems and marine wildlife. However, this literature is fragmented and can present conflicting or confusing conclusions, complicating policy analysis. For instance, some studies have found that diver experience reduces reef contacts,[192,250] while others have not.[197,198,234,251] Similarly, environmental dive briefings sometimes ameliorate reef contacts and damages,[188,194,236] but not always.[197] Likewise, female diving tourists performed better in some studies,[199] and worse in others.[192]

This study extends the literature in several key directions:

1. Our novel video-assisted methodology allows for simultaneous data collection of all human-reef and human-wildlife interactions on any given outing. This allows for the collection of comprehensive, time-varying, second-by-second data on reef socio-ecological interactions (e.g., social co-dynamics of the physical environment, wildlife, on-reef tourists, and tour guides) at an unprecedented level of granularity (over 1,000,000 units of observation).
2. We complement in-situ observations with a rich qualitative survey dataset of reef-related attitudes and behaviors, allowing for a comprehensive analysis of the drivers and characteristics underlying reef contacts and damages. These drivers include biases in subjects' attitudes and subsequent behaviors (e.g., the "illusory superiority" effect and the "Dunning-Krueger" effect) that have yet to be considered in this novel context.
3. We collect a host of individual- and group-level factors both at the diver level, and diver-second level, to holistically assess their relative contributions to reef contacts to inform reef conservation management and policy. This is crucial for informed

interventions, as the relative contributions of individual- and group-level factors to reef-damaging behaviors are the missing piece for adaptive, integrated, conservation management across all scales of intervention.

4. We also investigate the effects of operator eco-certification on on-reef tourists' and dive leaders' behaviors. Green Fins certification comprises tourists diving with Green Fins–certified dive operators (hereafter Green Fins tourists) and those diving with non-certified dive centers (non–Green Fins tourists). This will assess the degree to which Green Fins tourists make fewer reef contacts than do non–Green Fins tourists, and if so, how, why, and for what types of contacts (intentional vs. unintentional) and reef visitors (guests vs. guides). Previous studies have concluded that Green Fins appears conducive to reducing in-water reef contact rates,[233,234] but might also be mediated by the attitudes and behaviors of the tourists selectively choosing to dive with Green Fins operators.

A6.2: Extended Methods

A6.2.1: Site Inclusion Criteria

We conducted our study in Southeast Asia, a region which is historically neglected in reef impact studies despite simultaneously boasting the vast majority of the world's marine reef biodiversity and bearing the brunt of global on-reef tourism.[228] This study was conducted in direct collaboration with 36 Green Fins–certified and non-certified dive operators across five reef visitation hotspots in the Philippines (Logon, Dauin, and Panglao) and Indonesia (Bali

and the Nusa Islands). Indonesia and the Philippines are ranked first and second, respectively, as having the world's highest rates of reef tourism (Spalding et al., 2018).

Both archipelagic states are among the world's largest by population and area, and the diversity of visitation hotspots chosen for fieldwork within both countries offer a representative range of global tourism sites and operators that cater to a range of both local and international visitors. Additionally, from a comprehensive review of the literature, our study's results and subject demographics also seem largely representative of the regional and global on-reef tourist population (Table A6.1).

Table A6.1: *Summary of Existing Literature*
OW = Open Water; AOW = Advanced Open Water; DSD = Discover Scuba Diving; Pro = Divemaster or Instructor

Study	Country	Gender [N = Sample Size]	Contacts Min^{-1} (mean ± SE) [N = Sample Size]	Contact Intentionality Proportion from Contact Events	Dive Certification [N = Sample Size]
This Study	Indonesia & Philippines	Female (44.6%) Male (55.4 %) [N = 303]	0.259 ± 0.0188* [N = 440]	Accidental (61%) Intentional (39%)	OW (19.8%) AOW (45.6%) Rescue (12.7%) Pro (10.7%) [N = 338]
Zhang et al., 2023	Hong Kong (China)	Female (51.5%) Male (48.5%) [N = 398]	NA	NA	NA
Lee et al., 2022	Taiwan, Philippines, & Indonesia	Female (43.4%) Male (56.6%) [N = 1,800]	NA	NA	NA
PADI Certification Statistics , 2015-2020	Global	Female (37.3 %) Male (62.7%) [N ≅ millions]	NA	NA	NA
Lucrezi et al., 2019	Italy & Mozambique	Female (32%) Male (67%) [N = 499]	NA	NA	NA

Hammerton, 2017	Australia	Female (34.8%) Male (65.3%) [N = 400]	0.53 [N = 400]	Accidental (71%) Intentional (29%)	DSD (8.5%) OW (38%) AOW (23.5%) Rescue (11.8%) Pro (18.3%) [N = 400]
Giglio, et al., 2017	Brazil	Female (39%) Male (61%) [N = 94]	0.24 ± 0.05 [N = 94]	Accidental (94%), Intentional (6%)	NA
Roche et al., 2016	Philippines	Female (28%) Male (72%) [N = 100]	0.12 ± 0.01 [N = 100]	NA	OW (29.2%) AOW (37.1%) Rescue (9.00%) Pro (24.7%) [N = 89]
Toyoshima & Nadaoka, 2015	Japan	Female (55%) Male (45%) [N = 350]	0.53	NA	OW (41%) AOW (39%) Rescue (9%) Pro (11%) [N = 270]
Krieger & Chadwick, 2013	U.S.A.	NA	0.3 (estimate) [N = 240]	NA	NA
Chung et al, 2013	Hong Kong (China)	Female (34.2%) Male (65.8%) [N = 79]	0.568 [N = 81]	Accidental (74.1%) Intentional (25.9%)	OW/AOW (68.5%) Rescue (7.41%) Pro (24.1%) [N = 54]
Camp & Fraser, 2012	U.S.A.	Female (41%) Male (59%) [N = 83]	0.33 ± 0.06 [N = 83]	Accidental (55.4%) Intentional (44.6%)	NA
Ong & Musa, 2011	Malaysia	Female (42.4%) Male (57.6%) [N = 413]	NA	NA	NA
Di Franco et al., 2009	Italy	NA	0.36 [N = 108]	Accidental (76%) Intentional (24%)	NA

Luna et al., 2009	Spain	Female (27.1%) Male (72.9) [N = 181]	4.12 ± 0.355 [N = 181]	NA	Beginner (44.7%) Medium (42.0%) Expert (13.3%) [N = 181]
Worachananant et al., 2008	Thailand	Female (77%) Male (33%) [N = 108]	1.62 ± 0.19	NA	Beginner (41%) Novice (27%) Enthusiast (7%) Expert (25%) [N = 108]
Barker & Roberts, 2004	St. Lucia	Female (41.6%) Male (58.4%) [N = 353]	0.25 ± 0.04 (mean ± 95% CI) [N = 353]	Accidental (81.2%) Intentional (18.8%)	NA
Zakai & Chadwick-Furman, 2001	Israel	NA	0.407 (pooled mean) [N = 127]	NA	NA
Harriot et al., 1997	Australia	NA	2.08 (pooled mean)	NA	OW (64.0%) AOW (22.1%) Pro (14.0%) [N = 136]
Rouphael & Inglis, 1997	Australia	NA	0.541 ± 0.063 [N = 149]	NA	NA
Medio et al., 1997	Egypt	NA	0.211	NA	NA

*The *mean contacts per minute* metric is different from the *mean contact duration per minute* metric used in our study analysis. It was calculated and included here to match the format of other studies, but does not control for the length of time for which each contact occurs (no study prior to ours has accounted for this).

A6.2.2: Data Collection

From December 2022 to January 2024, we collected a host of in-situ visual censuses and post-dive questionnaires on scuba diving on-reef tourists across our study sites in the Philippines and Indonesia (Figure A6.1–A6.2, Table A6.2).

Table A6.2: *Sampling Effort Between Study Locations*

Region	Country	Total Dives Followed	Total Subjects Observed	Total Observation Hours	Total Subjects Surveyed
Bali / Nusa Islands	Indonesia	58	189	149	98
Logon	Philippines	49	161	107	96
Panglao	Philippines	28	90	73	43
Dauin*	Philippines	0	0	0	36
*No visual censuses conducted because coastal sites were primarily muck sites, not reef sites.					

A6.2.2.1: Video-Assisted Visual Censuses

We conducted in-situ, video-assisted visual censuses to quantify the frequency, timing, severity, and extent of underwater damages to coral reefs, along with a host of associated individual- and group-level features for each occurrence (Table A6.3). To quantify on-reef damages, researchers trailed behind scuba dive groups (3.26 ± 0.985 [mean ± SD] divers, excluding the researcher) and recorded video data of dive group tourists and tour guides for

the entirety of the dive using a high-resolution video camera.[1] Prior to and during the data collection process, tour groups were made aware of an ongoing research study related to reef conservation but were withheld additional details to minimize observer bias. All study protocols were conducted in accordance with the approved guidelines of the Institutional Review Board (IRB).

Following data collection, each dive's video footage was analyzed to generate a suite of individual- and group-level factors associated with each reef contact made by each diver during each dive (Table A6.3). Each reef contact per diver per dive was transcribed for its timing (timestamp for when in the dive it occurred); duration (difference between observation end time and observation start time); diver ID (which diver made the contact); damage type (e.g., no observed damage, sediment deposition, etc.); contact type (e.g., rest, drag, touch, etc.); contact substrate (e.g., coral); contact body part (e.g., fin); contact reason (e.g., support, bad finning, unknown, etc.); diver awareness and intentionality (i.e., intentional and aware, accidental and unaware, and accidental and aware); dive guide observation (binary); dive guide intervention (binary, and intervention type if applicable); and diver camera usage (binary). Each dive was also concurrently analyzed for each instance of a wildlife encounter, defined as any discernible interaction between any observed diver(s) and mobile or sessile marine life. Each wildlife instance was transcribed for its timing (timestamp); duration (difference between observation end time and observation start time); initial observer diver ID (diver ID of first wildlife spotter); participants' diver ID(s) (diver ID[s] of all divers involved

[1] This methodology mirrors those used in stereo video surveys for marine ecological monitoring, with the key differences being that a single camera is used instead of two (size estimates are unnecessary for this research) and that focal individuals are humans instead of fish assemblages.[252]

in the sighting); wildlife type (e.g., thresher shark, nudibranch, etc.); and the wildlife's position in the water column (i.e., on the reef or above the reef) (see Table A5.3 for detailed descriptions of each variable).

For each diver (individual level features), variables assessed included whether the diver was wearing gloves (binary); using a muck stick (binary); carrying and/or using a camera (binary, and camera type if applicable); and leading the dive (i.e., dive guest or guide). For each dive (group level features), variables assessed included the time, date, and duration of each dive; the dive site name (e.g., Kimud Shoal); dive site type (e.g., reef); and site geomorphology (e.g., wall dive); whether there was an environmental awareness message included in the pre-dive briefing (binary); the dive operator's name (e.g., Devocean Divers); the dive operator's Green Fins rating (e.g., Gold, Silver, Bronze, or Non-Member; Interested and Inactive ratings were used as controls); the total number of divers in the dive group (excluding the researcher); and the ocean current strength during the dive (i.e. 0 to 5 in increasing strength). Additional variables included the observer ID (which researcher filmed the dive); the coder ID (which researcher analyzed the video); and the country and region of where each dive took place (e.g., Logon Island in the Philippines).

Overall, this methodological approach allowed for both the simultaneous data collection of multiple subjects' underwater behaviors, as well as the ability to better control for inter-observer variability (multiple video coders could and did analyze the same video for training and verification). However, this approach also has several limitations. The first is the possibility for inter-coder variability in how each variable is interpreted, assessed, and subsequently transcribed from video to table. We controlled for this through the creation and

use of a video transcription protocol and extensive training, testing, and corroboration for output convergence between researchers, as well as through random quality control checks (independent transcription verifications for a random subset of video samples) conducted by the lead researcher (B.L.). An additional limitation is that assessing reef damages ex-post and through video, which can have limited coverage, likely results in conservative estimates of on-reef contact rates, and especially so for damaging contacts. The bar for discernible reef contacts and damages when observed through video is likely higher than when evaluated in-situ. This is because tourists can occasionally leave the camera frame and/or stray from the observer, making contacts, and especially reef-damaging contacts, harder to discern. As such, this sampling approach provides a conservative lower bound for the true number of reef contacts that actually occurred on each dive.

Table A6.3: *Full Variable List*			
	Column Name	Description	Format/Example
Fill per dive	**DIVE_ID**	*Individual dive identifier. The format is in "DATE", "TIME", "DIVE_SITE", and "DIVE_SHOP".*	E.g., "12-31-22_1346_KALANGGAMAN-WALL_EVOLUTION"
	CODER_ID	*The initials of the video coder.*	E.g., "BL"
	ENV_MESSAGE	*Indicates whether the dive briefing included a message about the environment or about pro-environmental behaviors.*	I.e., "1" (yes), "0" (no)
	CURRENT	*The current strength at each dive site, from 0 (no current) to 5 (heavy current).*	E.g., "3"
	DIVE_TYPE	*The type of dive performed that day. Multiple types are appended with underscore.*	E.g., "REEF", "MUCK", "WALL", "REEF_MUCK"
	VIDEO_ID	*The file name of each video being analyzed.*	E.g., "GX010003"
	TOTAL_DIVERS	*The number of divers being observed for analysis (excluding the researcher).*	E.g., "3"
	DIVE_START_TIME	*The start time (24-hour format) of each dive. Extracted from the researcher's dive computer.*	E.g., "13:46:03" in HH:MM:SS
	VID_START_TIME	*The start time (24-hour format) of the video. Extracted from the video camera's metadata.*	E.g., "13:48:00" in HH:MM:SS
	VID_DELAY	*The time delay (H:MM:SS) between the start of the dive and the start of the video.*	E.g., "0:00:02"
Fill per reef contact or wildlife encounter	**OBS_VID_TIME_START**	*The video timestamp for when the observation began. (Not time of day.)*	E.g., 0:00:40 in H:MM:SS
	OBS_DIVE_TIME_END	*The delay-adjusted dive time stamp for when the observation began. (Not time of day.)*	E.g., "0:00:42" in H:MM:SS
	OBSERVATION	*The observation type: either reef contact or wildlife sighting.* (Append with _UNCERTAIN if unsure)	I.e., "CONTACT", "WILDLIFE"
	WILDLIFE_TYPE	*Indicates the type of wildlife observed, as well as its position in the water column. "MACRO" indicates animals directly on the reef (e.g., nudibranchs, shrimps) and "MEGA" indicates free-swimming wildlife above the reef (e.g., sharks, turtles). "UNK" indicates unknown.*	E.g., "NONE", "SEAHORSE_MACRO", SHARK_MEGA", "UNK_MACRO"
	WILDLIFE_DURATION	*The duration of each wildlife sighting (H:MM:SS). Sighting begins when wildlife is first observed/pointed out and ends when wildlife disappears or when divers turn away.*	E.g., "0:01:12"
	WILDLIFE_SPOTTER	*Identifies the diver that finds or first points out the wildlife, if applicable. Uses the same identifying format for divers as shown below in DIVER_1, DIVER_2, etc.*	E.g., "GREEN-F_FEMALE_DM"
	DIVER_1		

	DIVER_2	*Indicates which diver(s) was involved in each reef contact or wildlife encounter. For reef contacts, only one cell is filled. For wildlife encounters, identifies all divers involved in the sighting. Fill out a brief descriptor (see example), and if diver is the dive guide, appends "DM" to the end.*	E.g., "GREEN-F_FEMALE_DM", "YELLOW-F_MALE"
	DIVER_3		
	. . .		
	DIVER_DM		
	CONTACT_SUBSTRATE	*The substrate with which the subject made reef contact.*	E.g., "CORAL", "MUCK", "SAND"
	CONTACT_TYPE	*The type of reef contact made by the subject.*	I.e., "NEAR-TOUCH", "LIGHT-TOUCH", "MEDIUM-TOUCH", "HEAVY-TOUCH", "DRAG", "HOLD", "REST"
	CONTACT_DURATION	*The duration (H:MM:SS) of each reef contact. Instantaneous and near touches are coded as "0:00:01".*	E.g., "0:00:12", "NA"
	CONTACT_AWARENESS	*Perceived diver awareness of each reef contact including both intentionality and awareness level. Uses best judgment to determine if it was accidental or intentional.*	I.e., "ACCIDENT-UNAWARE", "ACCIDENT-AWARE", "INTENTIONAL-AWARE"
	CONTACT_BODY_PART	*Body part making reef contact. Combines multiple body parts with an underscore.*	E.g., "FIN", "GAUGE", "CAMERA", "STICK", "HAND", "BCD", "LEG", "REG", "FIN_LEG"
	CONTACT_DAMAGE	*The level of observable damage from each reef contact. For near touches, the damage type will most likely be "SEDIMENT".*	I.e., "NO-OBS-DAMAGE", "SEDIMENT", "LIGHT-DAMAGE", "MEDIUM-DAMAGE", "HEAVY-DAMAGE"
	CONTACT_REASON	*Likely reason for each reef contact.Uses "UNKNOWN" appended with an underscore to code uncertainty.*	E.g., "NONE", "BAD-FINNING", "BAD-BUOYANCY", "SUPPORT", LOOSE-EQUIPMENT", "WILDLIFE", "OTHER-DIVER", "BALANCE", "CURIOSITY", DISTRACTED", "UNAWARE", "TRASH_CLEAN-UP", "UNKNOWN"
	CONTACT_DM_OBSERVE	*Indicates whether the dive guide (DM) observed the reef contact.*	I.e., "1" (yes), "0" (no), "NA" (DM themselves)
	CONTACT_INTERVENTION	*Indicates whether the dive guide (DM) intervened following the reef contact. "NA" if the DM did not observe the contact.*	E.g., "NA", "NONE", "SIGNAL" (hand signal), "TOUCH" (physical correction)
	USING_CAMERA	*Indicates whether the subject was using their camera when the reef contact occurred.*	I.e., "1" (yes), "0" (no)
	CAMERA_TYPE	*Indicates whether the diver involved was carrying a camera and, if yes, what type of camera was used.*	E.g., "NO-CAMERA", "POINT-SHOOT", "VID-CAMERA", "DSLR"
	MUCK_STICK	*Indicates whether the diver involved was carrying a muck stick (metal pointer).*	I.e., "1" (yes), "0" (no)
	GLOVES	*Indicates whether the diver involved was wearing gloves.*	I.e., "1" (yes), "0" (no)
	NOTES	*Additional comments, questions, or uncertainties.*	E.g., "Not sure if wildlife is MACRO or MEGA", "DIVER_3 left frame for 12 minutes and 13 seconds".

A6.2.2.2: Post-Dive Survey Questionnaires

Post-dive questionnaires were administered to on-reef tourists to assess subjects' demographic characteristics, their pro-environmental attitudes, perceptions of their own and other's underwater reef impacts and diving abilities, and matched survey response details. We disseminated laminated placards with a QR code linked to an online Qualtrics questionnaire across 36 dive operators in Indonesia and the Philippines from December 2022 to January 2024 (Figure A6.1). These placards were placed in prominent positions in all participating dive operators and were available for all subjects aged 18 and above to voluntarily complete once (one response per diver), after completing a dive. This survey was also presented to divers following all video-assisted underwater surveys to allow for matched assessments of perceived and actual underwater impacts. (A portion of the survey asked subjects if they dived with a Princeton University researcher and what distinguishing characteristics they had, allowing for data matching between subjects' observed and perceived reef impacts.)

The questionnaire itself was broken down into four sections: (1) Dive and Diver Information, (2) Perceived Underwater Impacts and Abilities, (3) Pro-Environmental Attitudes, and (4) Additional Background Information. The first section (1) consisted of questions regarding the subject's diving background (their diving experience and certification level), their most recent dive (where and when it happened), with what operator they chose and why, what equipment they brought on their dive, and whether they were accompanied by a Princeton University researcher during their dive (for matched observational analyses). The second section (2) inquired about a subject's perceptions of their own and other's underwater abilities (e.g., maintaining buoyancy control) and damages (number of intentional and

accidental reef contacts). The third section (3) assessed the strength of the subject's pro-environmental social norms by asking about their level of compulsion and embarrassment towards performing or being seen performing certain reef-related behaviors.[217] Namely: maintaining buoyancy control, telling others not to touch corals, feeding fish, swimming close to large marine animals, touching large marine animals, picking up garbage from the sea floor, taking pieces of dead coral, breaking off pieces of live coral, removing shells from the reef, telling others not to anchor boats on coral, swimming close (<1 m) to the reef, intentionally making physical contact with the reef, and accidentally making physical contact with the reef. The final section (4) consists of demographic questions regarding a subject's country of origin, country of residence, gender, age, highest level of education, income level, and additional survey feedback (Figures A6.9–A6.13).

A6.3: Data Processing

A6.3.1: Video-Assisted Visual Censuses

We created a dataset with the aggregate number of intentional, accidental, and total reef contacts made by each diver on each dive. To account for variable durations of both contact and dive time, we converted raw contact counts into contact rates (mean contact duration per minute of diving). We converted discrete reef contacts made by each diver into four variables: mean total reef contact duration per minute of diving, mean intentional reef contact duration per minute of diving, mean accidental reef contact duration per minute of diving, and mean damaging reef contact duration per minute of diving (Table A6.4).

Table A6.4: *Reef Contact Rates by Intentionality and Damage*				
	Mean Contact Duration Per Minute of Diving (seconds per minute ± SD)			
Data Subset (n = # subjects)	All Contacts	Intentional Contacts	Accidental Contacts	Damaging Contacts
Total (n = 411)	1.96 ± 4.30	1.31 ± 3.27	0.646 ± 1.87	0.574 ± 1.38
Indonesia (n = 177)	1.01 ± 2.34	0.679 ± 1.80	0.330 ± 1.05	0.318 ± 1.10
Philippines (n = 234)	2.68 ± 5.22	1.79 ± 3.99	0.885 ± 2.28	0.767 ± 1.54
Green Fins (n = 239)	1.85 ± 4.48	1.27 ± 3.75	0.586 ± 1.52	0.546 ± 1.44
Non–Green Fins (n = 172)	2.11 ± 4.05	1.38 ± 2.49	0.729 ± 2.27	0.612 ± 1.31
	Mean Number of Contacts (mean number ± SD)			
Data Subset (n = # subjects)	All Contacts	Intentional Contacts	Accidental Contacts	Damaging Contacts
Total (n = 411)	11.4 ± 16.9	4.43 ± 9.07	6.94 ± 11.1	4.54 ± 8.24
Indonesia (n = 177)	7.96 ± 13.4	2.94 ± 6.57	5.02 ± 9.86	2.31 ± 7.27
Philippines (n = 234)	14.0 ± 18.7	5.56 ± 10.4	8.40 ± 11.7	6.22 ± 8.53
Green Fins (n = 239)	8.91 ± 11.3	3.11 ± 5.56	5.79 ± 8.24	4.01 ± 6.72
Non–Green Fins (n = 172)	14.8 ± 22.0	6.27 ± 12.2	8.54 ± 13.9	5.26 ± 9.95

A6.3.2: Post-Dive Survey Questionnaires

We created a composite environmental score for each survey respondent by aggregating the mean scores for survey responses to feelings of compulsion and embarrassment towards various reef-related behaviors (see section [3] above). We excluded responses to "swimming close (<1 m) to the reef", as this statement did not indicate social norms either for or against conservation. Based on these responses, each diver was assigned a composite environmental score out of a possible 8.0 points, with 8 being the most pro-environmental (Figure A6.3).

A6.3.3: Matching Procedures

We matched survey responses to observational data to allow for comparisons between perceived and realized underwater impacts of individual on-reef tourists. We did this through dive and questionnaire survey metadata and responses to our question from our survey respondents [i.e., "Did you dive with a Princeton University researcher on this dive?" and "What color were your fins? (Or other distinguishable characteristics underwater?)"]. Coupling these data with behavioral and questionnaire survey metadata (e.g., date and time of completion, researcher notes, etc.), we created a unique "DIVER_ID" for every definitive match between observational and questionnaire survey subjects for downstream analysis.

A6.3.4: Panel Data Processing

We construct a panel dataset for use in evaluating the effects of within-dive drivers of reef contacts. We let variable y_{itd} be a binary variable that equals 1 during a reef contact and 0

otherwise, where i refers to a diver, t refers to the number of minutes since that diver started their dive, and d refers to the group of divers on the same outing (a dive). While the native temporal resolution of our data is at the dive-second level, we collapse these data to the minute level for simplicity.

A6.4: Data Analysis

Using the methodological approaches outlined above, we compare subjects' self-reported perceptions of their underwater impacts with their observed impacts, and use machine learning models and other statistical approaches to assess the contributions of a wide range of individual- and group-level factors to intentional and unintentional reef contacts and damages. This allows for an integrated approach to quantifying reef visitation damages.

A6.4.1: Matched Survey-Observation Comparisons

To compare subjects' observed underwater impacts with their perceptions of their underwater impacts, we subsetted our observational and survey data to only include subjects with matched observations/responses in both datasets. We find no significance difference in the mean total reef contact duration per minute of diving ($t(117) = -0.815, p = 0.417$), the mean intentional reef contact duration per minute of diving ($t(132) = -1.63, p = 0.106$), the mean accidental reef contact duration per minute of diving ($t(108) = 0.649, p = 0.517$), and the mean damaging reef contact duration per minute of diving ($t(139) = -0.593, p = 0.554$) between data subsets. Matched and unmatched survey subjects also displayed no significant differences in their composite environmental scores ($t(130) = 0.536, p = 0.593$), self-

perceived total reef contacts ($t(171) = 0.281, p = 0.779$), self-perceived intentional reef contacts ($t(177) = 0.475, p = 0.635$), self-perceived accidental reef contacts ($t(145) = 0.132, p = 0.895$), as well as basic demographic information (e.g., education [$t(140) = -0.712, p = 0.478$], income [$t(184) = -1.02, p = 0.311$], and age [$t(151) = 0.206, p = 0.837$]). Overall, these results lend credence to our assumption that our matched subset of survey respondents are likely not unrepresentative of our overall dataset.

We subtracted divers' self-reported underwater impacts with their observed underwater impacts (e.g., the difference between a subject's self-perceived number of total reef contacts and the total number of reef contacts they were observed to make). Survey respondents were also asked to assess their underwater impacts and abilities as a relative function (e.g., "below average", "average", and "above average") compared to all other divers, all other divers of the subject's dive certification level, and all other divers currently diving with the subject on their last dive. Together, these questions helped to pinpoint divers' perceptions of their underwater abilities while controlling for potential biases in which divers might have access to the survey (e.g., in case certain dive sites or operators disproportionately cater to a specific diver demographic). Comparing these responses with what one might expect from a symmetric distribution thus allowed us to detect systematic biases in divers' self-perceptions of their relative underwater abilities (Figures A6.4–A6.8).

A6.4.2: Random Forest Machine Learning Models

We normalized candidate features and used random forest machine learning algorithms to assess the contributions of individual- and group-level factors contributing to total,

intentional, and accidental reef contacts. For each feature, we calculated its mean decrease accuracy (%IncMSE), variable inflation factor, and partial dependence plots (with bootstrapped 95% confidence intervals) relative to random noise and compared each model's R^2 and RMSE between training and testing datasets (split at 0.7) using the "Boruta", "caTools", "Metrics", "randomForest", and "regclass" packages in R v4.3.3.

A6.4.3: Causal Inference Analyses for Wildlife Sightings

We next investigated the relationship between wildlife sightings and reef contacts, motivated by its prominence in our random forest analysis. The associative correlations highlighted by the random forest analysis do not by themselves show that wildlife sightings directly cause reef contacts. For example, it could be that the reef tourists experiencing more wildlife sightings also recreate at sites with significantly more underwater currents. To control for potential time-varying and -invariant confounders, we employed stringent fixed effects and used our high-resolution data to isolate the effect of wildlife sightings *per se* on reef contact rates in our individual- and group-level dataset.

First, we let w_{itd} refer to a binary variable that equals 1 in periods in which diver i observed wildlife, and 0 in periods in which diver i did not. We let α_i represent a diver fixed effect, which controls non-parametrically for any time-invariant features of a diver that could affect their reef contact probability (e.g., underwater expertise and experience, internal proclivity toward touching coral, etc.), and α_{td} to denote a dive-minute fixed effect, which controls for any feature of the dive condition simultaneously experienced by all divers (e.g., a

surge current simultaneously experienced by all tourists). Then, we can estimate the following model:

$$\text{M1: } y_{itd} = \beta w_{itd} + \alpha_i + \alpha_{td} + \varepsilon_{itd}$$

In this model, our estimate for β represents an estimate for the change in the probability that a diver will touch the reef that is caused by a wildlife sighting. β has a causal interpretation under the assumption that conditional on the included fixed effects, the wildlife sighting variable is exogenous. This is highly plausible in this context, given there is inherent randomness in which divers in a particular minute of the dive happen to be able to see wildlife. That is, minute by minute, there is plausibly exogenous variation in which members of a dive group are participating in a wildlife sighting and which are not.

Notably, identification of β in M1 comes through variation in wildlife sightings across individuals within a particular minute of a dive, data that we specifically collect during our video transcriptions (Table A6.3). Our stringent fixed effects control not only for all time-invariant factors that might affect the probability of diver i touching the reef, such as their levels of diving experience and expertise, background demographic factors, intrinsic pro-conservation attitudes, and physical condition, but also for any time varying within-dive confounders, such as co-occurring changes in current, diving depth, and other within-dive conditions.

In Table A6.5, we present estimates from variants of M1 using an OLS fixed effects regression, but also consider estimation of a model with the same conditional mean assumption using Poisson Pseudo-MLE as a robustness check. When estimating uncertainty, we allow for

arbitrary correlations both across time and within a dive, in the unobserved error by using a clustered standard error estimator, clustering at the d level.

Table A6.5: *Variations of M1 Estimates*

Column M1.0 presents the results from estimating M1 above using OLS. Column M1.1 estimates a model with the same RHS as M1, but assuming the LHS is E(log(y)), using Poisson Pseudo Maximum Likelihood, and thus the coefficient estimate has an interpretation as a proportional increase. This model uses fewer observations, as it only uses data in which there are some non-zero outcomes within a fixed effect group. M1.2 estimates M1 but with less stringent fixed effects, including only a diver fixed effect, and a minute of dive fixed effect. M1.3 augments M1.0 to include a lead and lag of the wildlife indicator.

	M1.0	M1.1	M1.2	M1.3
Wildlife	0.193***	1.211***	0.154***	0.181***
	(0.025)	(0.140)	(0.014)	(0.025)
Wildlife Lead				0.022
				(0.016)
Wildlife Lag				0.032•
				(0.018)
Num.Obs.	20656	6335	20656	19748
Std.Errors	by: dive_id	by: dive_id	by: dive_id	by: dive_id
FE: i	X	X	X	X
FE: minute^dive_id	X	X		X
FE: minute			X	

*• $p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Clustered standard errors are in parentheses.*

We find that a wildlife sighting increases the probability of reef contact by about 19 percentage points, which corresponds to more than a 100% increase relative to periods without sightings. This result is highly statistically significant, and robust across a variety of specification choices. To investigate the possibility of delayed effects (i.e., wildlife sightings preemptively or belatedly resulting in reef contacts), we also estimate a version of M1 that includes leads and lags of the treatment variable, w_{itd}. Overall, we find that the treatment effect is concentrated in the contemporaneous period, and that the coefficients on the lead and lag terms are statistically insignificant and small.

Overall, we find strong evidence that wildlife sightings cause a significant but temporary elevation in the likelihood that a diver will contact the reef. This finding is robust across a variety of specifications. In Table A6.6 below, we present estimates of M1 with a variety of different outcome variables. Column 1 reproduces the estimate from Column 1 of in-text Table A6.5. Columns 2, 3, and 4 replace the outcome variable with an indicator that reflects whether a diver had an intentional, unintentional, or damaging contact in any given minute. In the row "Effect as a proportion of dep.var mean", we present the coefficients from the row above normalized by the mean of the dependent variable. Overall, we find that wildlife significantly increases all types of reef contact, but intentional contacts are affected the most, both in absolute terms, and relative to the mean number of the intentional contacts in the sample.

Table A6.6: *M1 Estimated Using Various Outcome Variables*

Contact type	Any	Intentional	Unintentional	Damaging
Wildlife	0.193***	0.150***	0.070***	0.062***
	(0.025)	(0.023)	(0.018)	(0.015)
Effect as proportion of dep.var mean	1.4104	2.1970	0.85381	1.0574
Std.Errors	by: dive_id	by: dive_id	by: dive_id	by: dive_id
FE: i	X	X	X	X
FE: minute^dive_id	X	X	X	X

• *$p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Clustered standard errors are in parentheses.*

A6.4.4: Behavioral Co-Dependence Analyses

We next implemented specifications that aim to test whether the *behavior* of other divers on the same dive affect diver i's likelihood of reef contact. To do so, we construct a binary variable, y_{itd}^{other} which is equal to 1 for diver i in minutes in which another diver in their

dive is touching the reef and 0 otherwise. Table A6.7 presents breaks our diver-minute level dataset into four categories, based on the values of y_{itd}^{other} and w_{itd}:

Table A6.7: *Breakdown of All Possible Wildlife and/or Contact Categories*

	Proportion of Sample	Contact Probability
No Wildlife or Others Touching	0.606	0.08
No Wildlife and Others Touching	0.182	0.152
Wildlife without Others Touching	0.121	0.231
Wildlife and Others Touching	0.091	0.359

Above, we see that for most of the diver-minutes (~60%), there are no wildlife sightings and no other divers in the group touching the reef. In these periods, the probability that diver i touches the reef is around 1%. However, this probability more than doubles during the ~18% of periods in which there is still no wildlife, but others are touching the reef. Periods in which there is both wildlife and other people touching demonstrates an even higher probability of diver i making reef contact, at 35% probability. Given that this approach does not account for unobserved confounders that might increase the likelihood of all members of a dive group touching the reef simultaneously (e.g., a sudden change in ocean current), we attempt to further isolate the relationship between the behaviors of other divers and those of diver i.

While we are not able to employ the stringent fixed effects we use in M1 when analyzing behavioral co-dependence, given near perfect multicollinearity (i.e., controlling for a dive-by-minute fixed effect is similar to controlling for the total of touches of other divers to begin with), we can still estimate a modified version of M1:

$$\text{M2:} \quad y_{itd} = \beta_1 w_{it} + \beta_2 y_{it}^{others} + \beta_3 w_{it} \cdot y_{it}^{others} + \alpha_i + \alpha_t + \varepsilon_{itd}$$

Relative to M1, we make two changes. Firstly, we introduce y^{others}, the explanatory variable of interest. Second, we alter the fixed effects, replacing the dive-minute fixed effect with a simple dive time fixed effect (i.e., the minutes since the start of each dive), due to the multicollinearity issue mentioned above. We retain the wildlife control variable, an obvious potential confounder, and also include an interaction of the other contact variable and our wildlife sighting variable, saturating the model with the four mutually exclusive and exhaustive categories listed in Table A6.7 above.

Table A6.8 below shows results from estimating varieties of M2. The reference category, in which diver i does not see any wildlife and no other divers in the group are touching the reef, is omitted. Overall, we find that other divers touching the reef are associated with additional reef contacts, both during periods with wildlife sightings and periods without them, corroborating our associative finding of behavioral co-dependence (i.e., that one's reef contacts *per se* result in other's reef contacts and vice versa) (Figure 6.2).

Table A6.8: *M2 Estimates*

M2.1 presents an estimate for M2 using OLS, without including any fixed effects. M2.2 presents OLS estimates of M2 above. M2.3 assumes a log functional form for the outcome variable and estimates the outcome variable using Poisson Pseudo-MLE.

	M2.1	M2.2	M2.3
No Wildlife and Others Touching	0.152***	0.052***	0.482***
	(0.013)	(0.011)	(0.079)
Wildlife and Others Touching	0.359***	0.220***	1.094***
	(0.025)	(0.020)	(0.078)
Wildlife without Others Touching	0.231***	0.131***	0.872***
	(0.022)	(0.017)	(0.073)
Num.Obs.	20577	20577	16752
Std.Errors	by: dive_id	by: dive_id	by: dive_id
FE: i		X	X
FE: minute		X	X

• *$p < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Clustered standard errors are in parentheses.*

Overall, we find that other divers touching the reef is associated with a large and statistically significant increase in one's own reef contact probability, both in and out of the presence of wildlife. The key threat to identification (our ability to isolate the causal effects of other on-reef tourists' reef contacts on our own) here is that periods in which divers face increased exposure to unobserved confounding variation show elevated reef contact rates for all divers. Such a confounder could be an unaccounted pathway that affects the values of both y_{others} and y_i.

However, from the knowledge gained by extensive field work, we do not believe that there are many candidates for confounding variation, most of which can be plausibly ruled out:

1. The co-occurrence of wildlife observations during a reef outing might mediate reef contact co-dependence. Indeed, we offer causal evidence for this above. Here, we also control for concurrent wildlife sightings in our analysis, ruling this out as a confounder.
2. The timing of a dive might be a significant predictor of reef contacts, with contacts generally clustering toward the beginning and end of dive outings.[197,234] We completely

control for dive time in our analysis using the "dive minute" fixed effect, α_t, ruling this out as a confounder.

3. The moment-by-moment changes in ocean current (e.g., swells) throughout a dive. As current data is collected on the dive-level, within-dive changes in current would not be captured in these data. As a precaution, we repeated (and replicated) our analysis with one site, Manta Point in Nusa Penida, Indonesia, both included and excluded from consideration given its consistent swell currents.
4. Reef tourists in a dive group tend to (and should) keep to roughly the same depth as each other during each dive; the closer this depth is to the reef/benthos, the more likely that unintentional contacts are to occur. Our analyses were repeated (and replicated) by filtering out unintentional reef contacts to partially control for the by-products of underwater depth (i.e., divers being too close to the reef often make accidental contacts), which yielded qualitatively identical results.

In the absence of plausibly exogenous variation in the reef contacts of other co-recreating tourists, our results are indicative of a causal relationship in underwater behavioral co-dependence and suggest that the likelihood of large, omitted variable bias in M2 is small. Overall, our data clearly shows evidence of high levels of clustering in the contact rates amongst divers on the same dive. We posit that social norms are consistent with our statistical and field work evidence and seem likely to explain at least some of this clustering. Further causal analysis could further explore this channel in future research.

A6.5: Figures

Figure A6.1: *Breakdown of Observational, Questionnaire, and Matched Survey Data Collected*

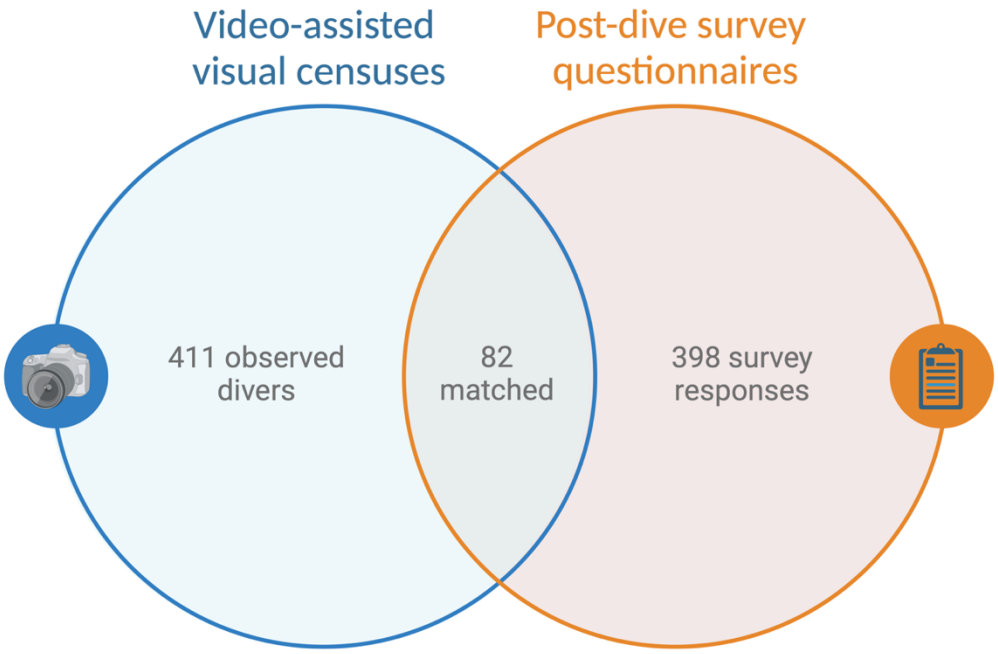


Figure A6.2: *Sampling Effort Across Countries and Tour Operators*

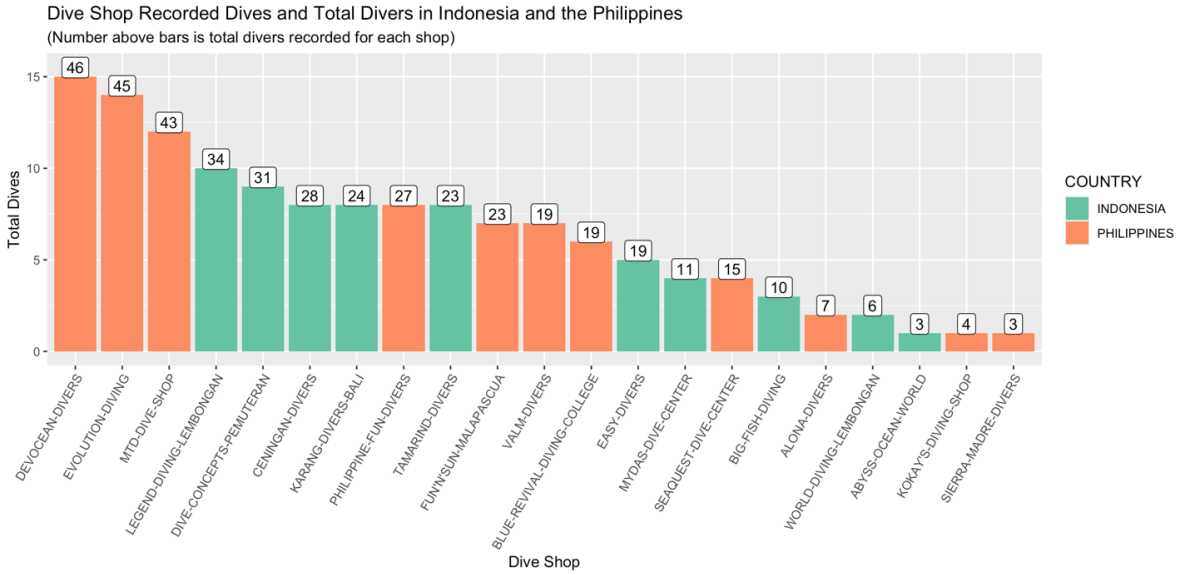


Figure A6.3: *Composite Environmental Score Spread of Survey Respondents*

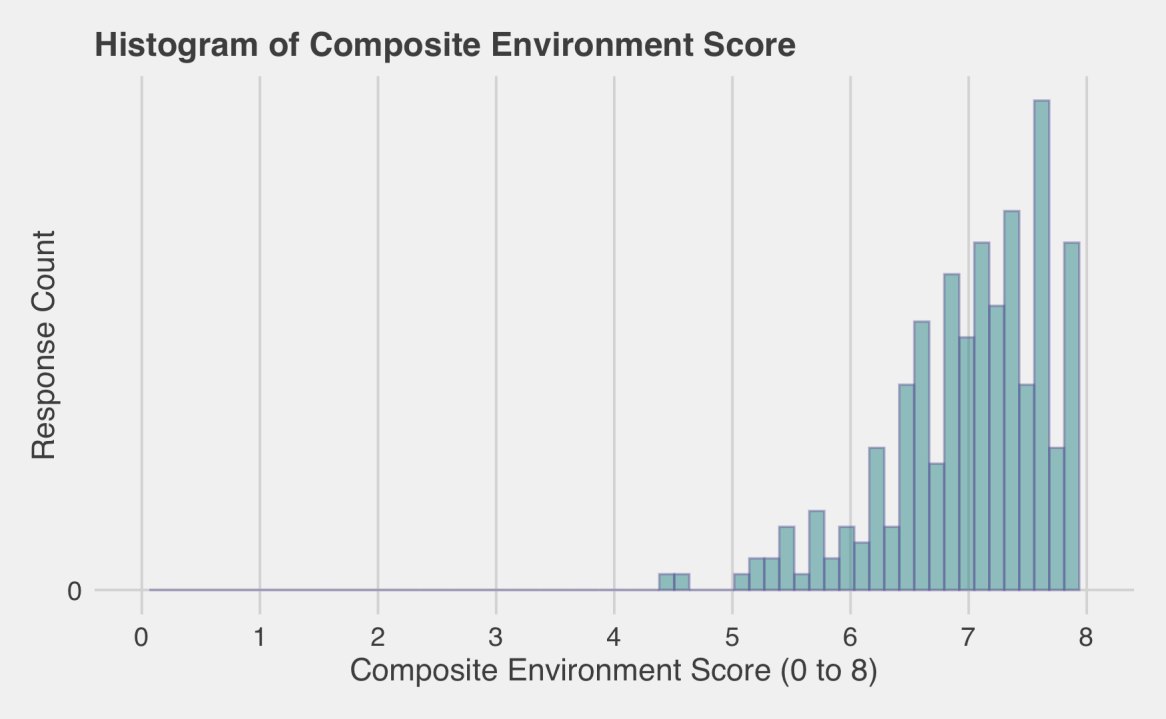


Figure A6.4: *Self-Perceived Ability of Divers to Avoid Intentional Reef Contacts*

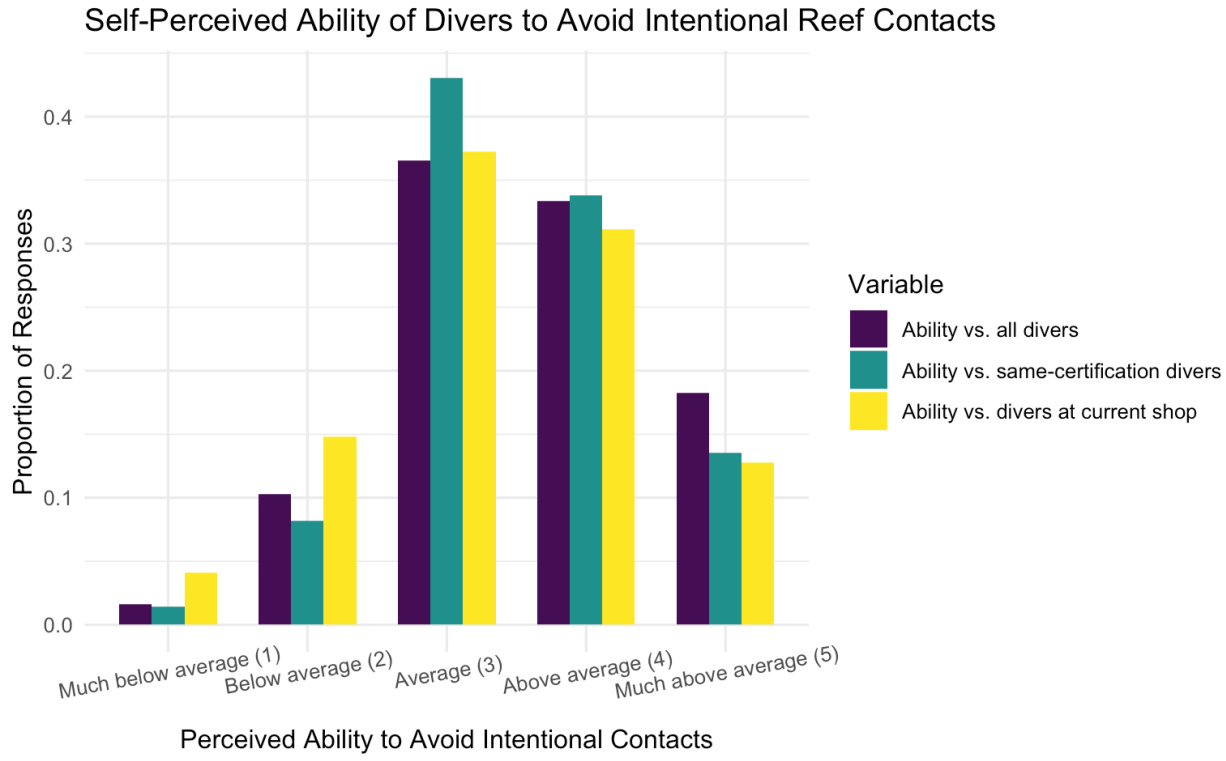


Figure A6.5: *Self-Perceived Ability of Divers to Avoid Accidental Reef Contacts*

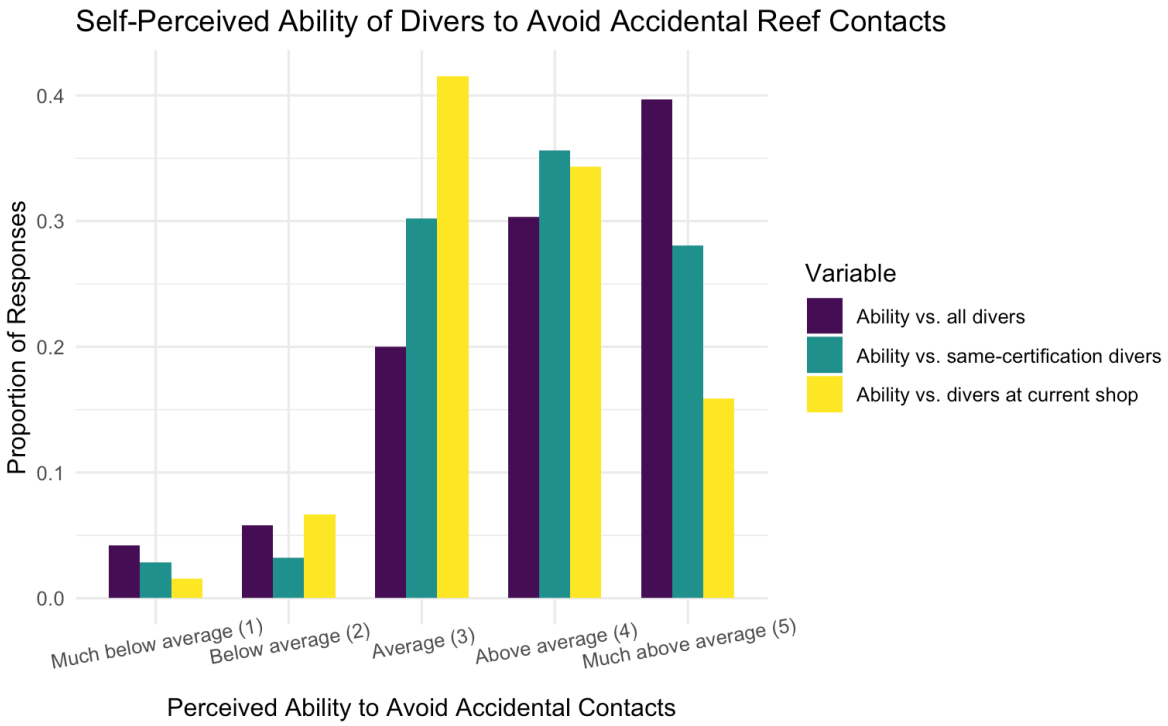


Figure A6.6: *Self-Perceived Ability of Divers to Maintain Buoyancy Control*

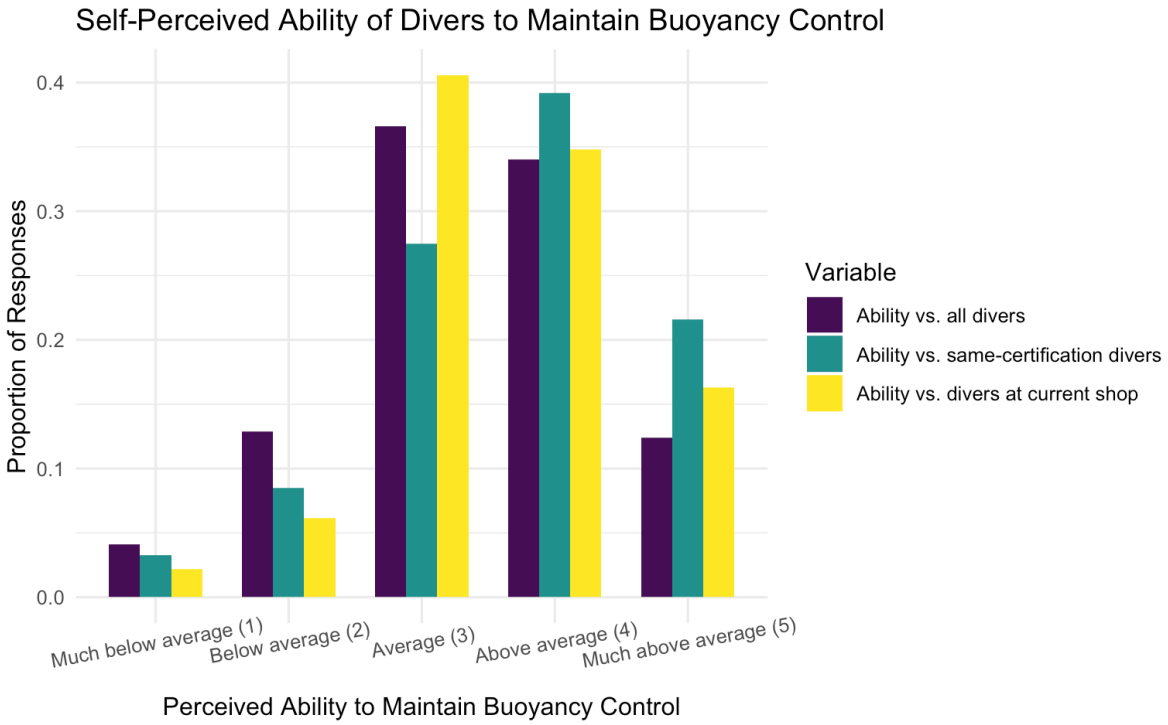


Figure A6.7: *Overconfidence Effect in On-Reef Tourists*

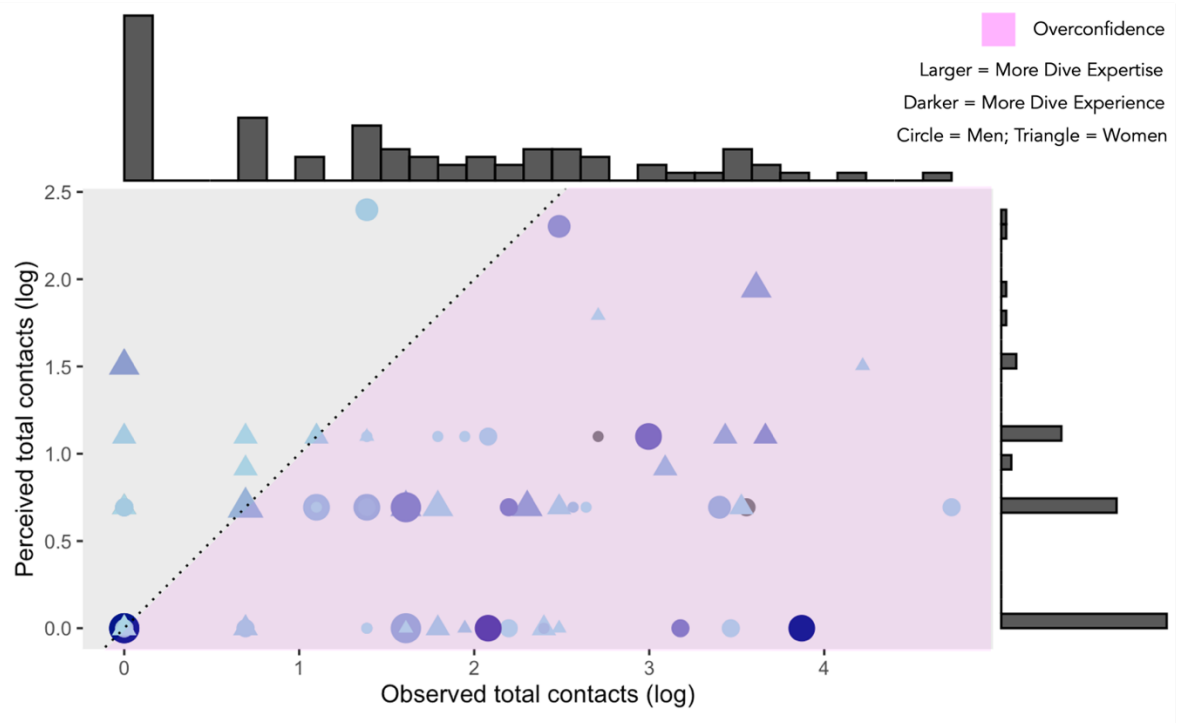


Figure A6.8: *Dunning-Kruger Effect in Divers for all Types of Contacts*

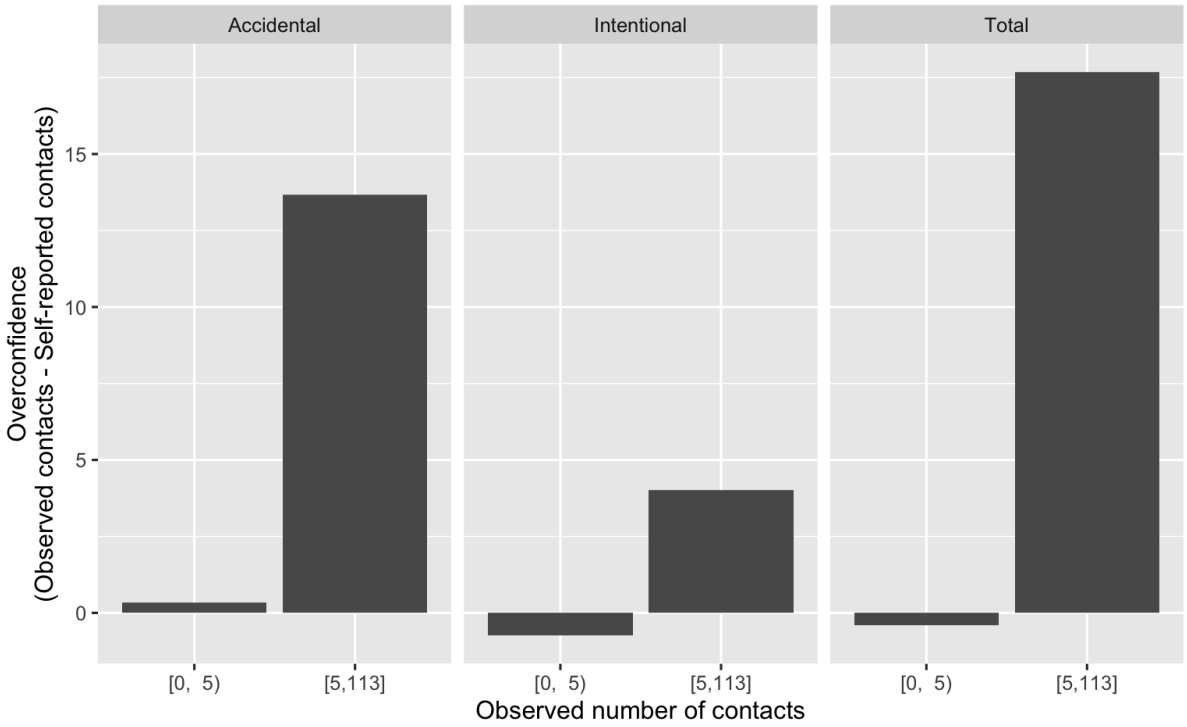


Figure A6.9: *Top 20 Countries of Origin for Survey Respondents*

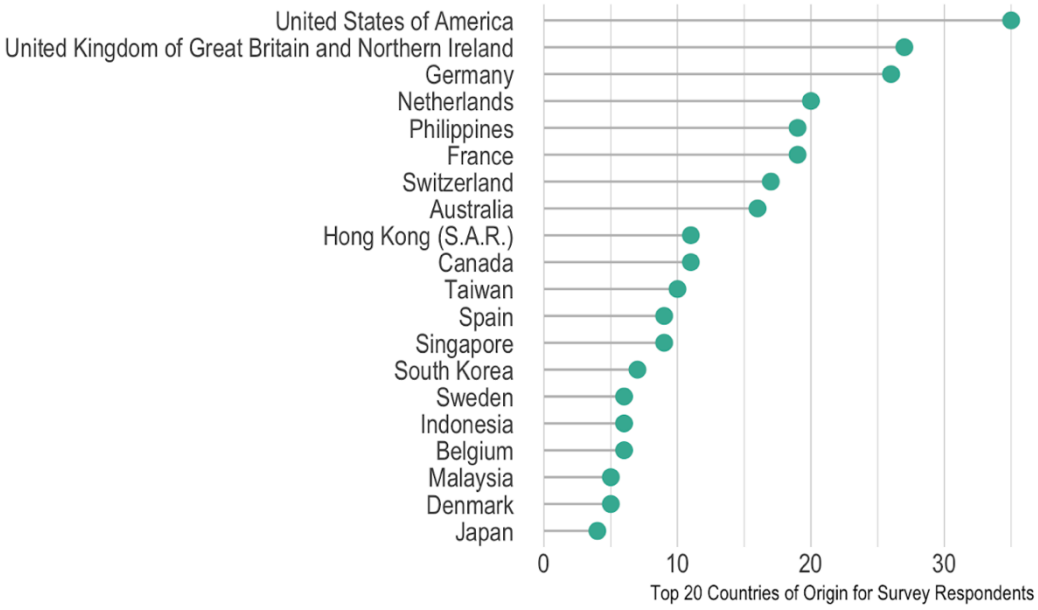


Figure A6.10: *Top 20 Countries of Residence for Survey Respondents*

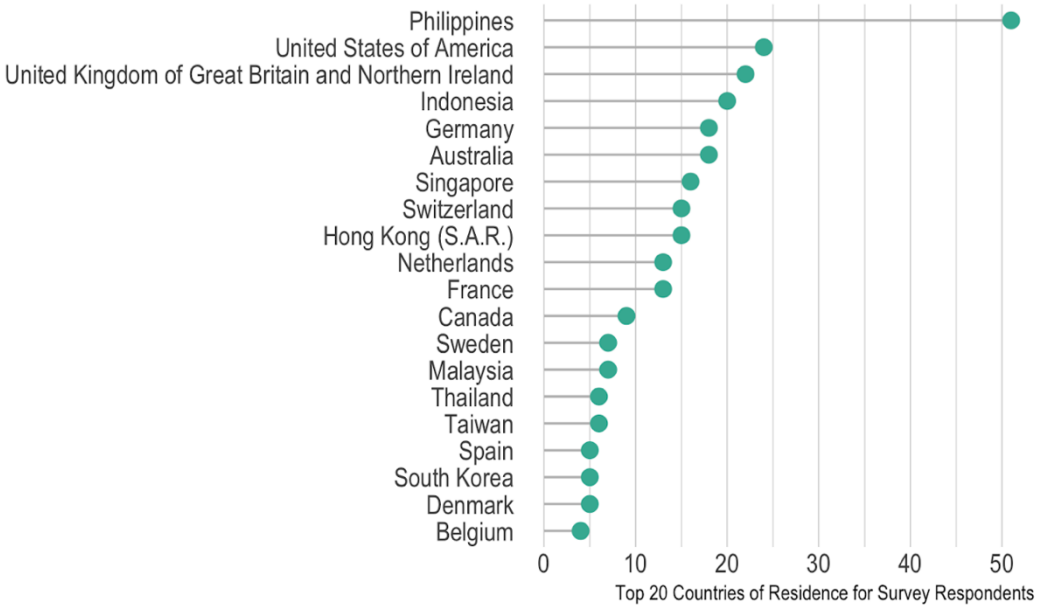


Figure A6.11: *Gender Breakdown for Survey Respondents*

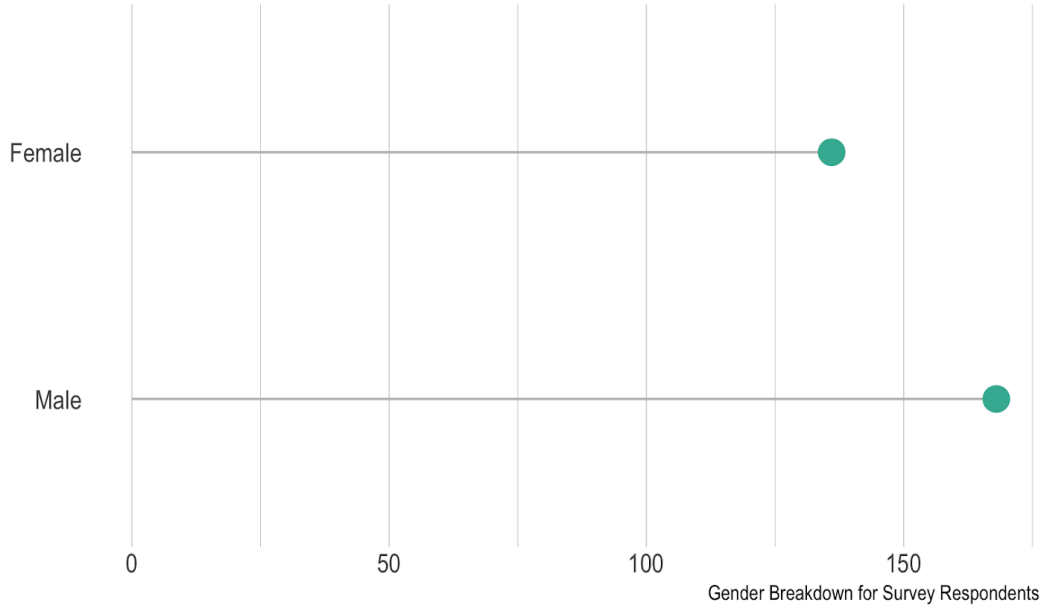


Figure A6.12: *Income Breakdown for Survey Respondents*

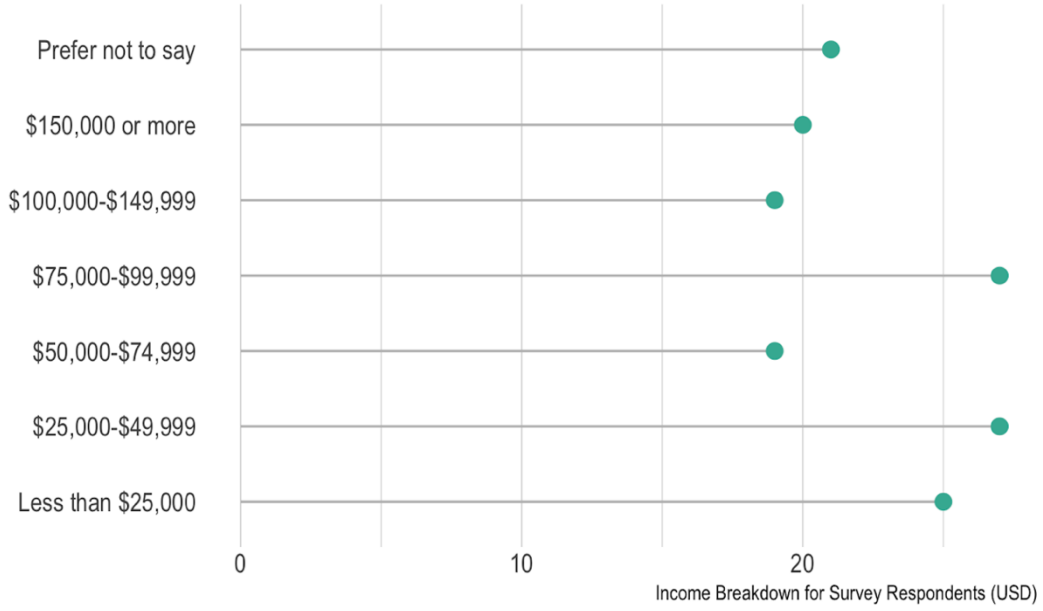
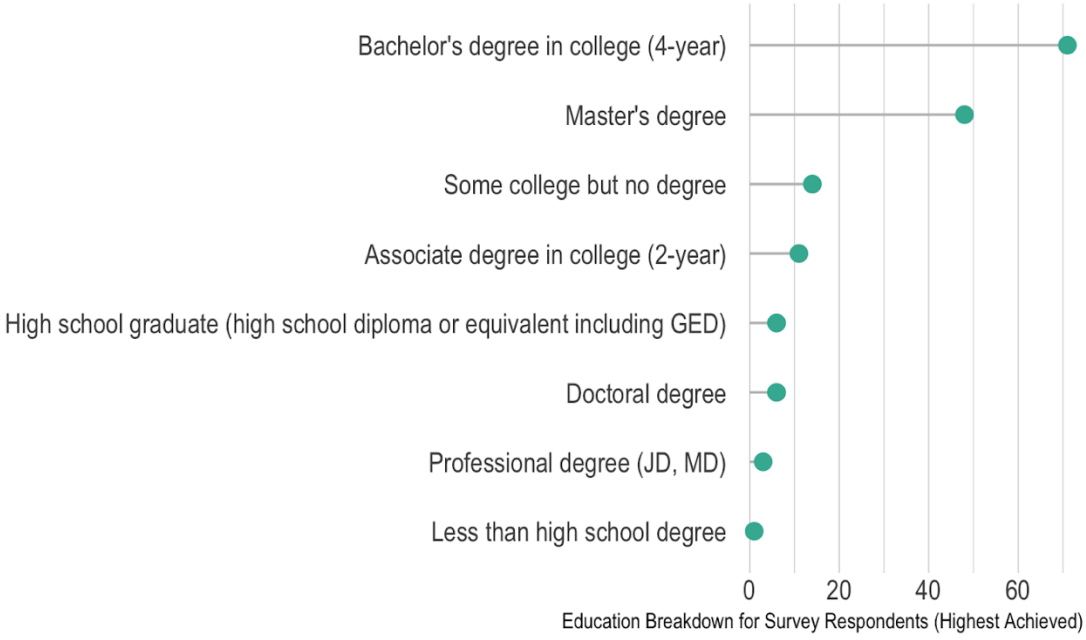


Figure A6.13: *Education Breakdown for Survey Respondents (Highest Achieved)*



Chapter 7 — Conclusion

7.1: Summary of Research Findings

Chapters 2 to 6 explore the intersection of human behavior, the biosphere, conservation ecology, and policy, underscoring the inherent trade-offs between maintaining biodiversity and addressing human-centric needs. The dissertation navigates these complexities by presenting an integrative focus on tailored regulation and pro-conservation behavior change, all while attending to the competing goals stakeholders and decisionmakers often face.

Chapter 2 presents a robust framework to define and categorize "wet markets" in the context of their variegated risks to human health and biodiversity. By systematically analyzing risk factors across different wet market types, I underscore the critical need for tailored regulatory approaches that address specific risks without compromising food security or cultural alimentary practices integral to local communities. Crucially, I emphasize the variability among wet markets and stress the importance of recognizing their vital role in food provisioning, livelihoods, and cultural identity for millions of people globally. Thus, a taxonomy of wet market risks enables decisionmakers to differentiate between markets that pose higher risks of zoonotic disease transmission and biodiversity loss and those that pose lower risks, as well as to implement tailored regulations that are commensurate to these variable risks.

Chapter 3 concerns the online marine aquarium fish trade in the United States, and shifts focus to an opaque industry in which regulations are insufficiently implemented and enforced. I conduct a comprehensive web-scraping study of four major online e-commerce platforms selling ornamental marine fish in the United States and collate data on fish taxa, prices, and sourcing methodology (wild-caught vs. captive-bred) to examine how consumer

behavior and market dynamics might impact fish biodiversity. Overall, I find 660 unique fish species available for sale across these platforms, with a significant 88.9% of these species being sourced exclusively from wild populations. Such a high reliance on wild-caught fish raises substantial conservation concerns, particularly given that 39 of the species identified were of conservation concern, according to the IUCN, with 32 of these species sourced solely from the wild. This underscores the urgent need for enhanced regulatory scrutiny and sustainable practices within the trade. I also find that retail prices are significantly correlated with various socio-ecological factors, including the fish's source (captive-bred vs. wild-caught), body length, minimum occupied depth, and schooling behaviors. Finally, I identify substantial data gaps and note 153 species for sale online that are not listed in either Fishbase or the IUCN, two authoritative databases of species traits. This indicates a significant deficiency in current databases and emphasizes the need for more comprehensive and updated information to facilitate better management and conservation strategies.

Chapter 4 connects human recreational activities, namely tourism, with environmental degradation, emphasizing the dual role that coastal visitation plays in both benefiting from and harming coral reefs. Leveraging high-resolution live coral cover maps, advanced web-scraping techniques, and machine learning models, I quantify the co-occurrence of tourism and live coral cover across the main Hawaiian islands and provide a macro-scale view of the ecological impacts of reef tourism. This approach provides a detailed snapshot of tourist visitation patterns, revealing correlations between visitation rates and indicators of coral reef health such as live coral cover, water quality, and site accessibility. Overall, I find that higher live coral cover attracts more on-reef visitation, illustrating the economic value of healthy reefs to

tourism. However, this positive relationship is counterbalanced by evidence that concentrated visitation at popular sites contributes to the subsequent degradation of the site's nearshore coral cover. These feedback loops suggest that while tourism may economically benefit from pristine reef environments, it also poses a threat to their long-term sustainability.

In Chapter 5, I then bridge the gap between macro and micro by examining recreational scuba diving impacts on coral reefs. This chapter illustrates the interplay between individual human behaviors (micro) and broader conservation policy goals (macro), pointing to regulatory reforms that can prevent reef degradation while promoting sustainable tourism. I critique existing voluntary approaches aimed at reducing reef contacts, such as eco-certification schemes and voluntary dive standards. While acknowledging their localized successes, particularly in promoting "no-touch" policies among dive operators and divers, I argue that these initiatives often lack sufficient long-term incentives and enforceability to achieve widespread compliance. I then explore the potential of policy frameworks within Marine Protected Areas (MPAs) to effectively mitigate reef damage. I advocate for the implementation of regulatory measures, including the establishment of policy safeguards (e.g., reef "safety bubbles") to prevent unintentional contacts, that are tailored to the unique conditions and conservation needs of individual MPAs. Drawing parallels with successful policy interventions in other domains, such as anti-smoking laws and seat belt regulations, I emphasize the importance of formal regulations to establish clear social norms and expectations, driving systemic behavioral change among divers. By fostering a culture of responsibility and environmental stewardship among divers, reinforced by formal regulations, I underscore the

underutilized role of policy change to propagate social norm change wherever recreational diving activities occur.

Finally, in Chapter 6, I employ primary data on diver behaviors in Southeast Asia to assess the micro-level actions that contribute to reef degradation. Using novel mixed-method observational and questionnaire survey techniques, I reveal the complex dynamics influencing reef damage caused by on-reef tourists across dive sites in Indonesia and the Philippines. Coupling observations of tourists' behaviors underwater, including a quantification of their reef contacts and damages, and a subsequent assessment of divers' attitudes and perceptions through comprehensive surveys, I find a substantial gap between perceived and actual impacts on coral reefs. Tourists consistently overestimate their diving abilities and underestimate their reef contacts, reflecting cognitive biases including the illusory superiority and the Dunning-Kruger effects in a novel context. Another pivotal finding of the chapter is the identification of unintentional and unnoticed damages (UUD) as a predominant driver of reef-damaging behaviors, comprising over 60% of all observed reef contacts. This insight underscores the importance of addressing inadvertent impacts through targeted interventions aimed at enhancing diver awareness and skills. I highlight the influence of social norms and peer behaviors on tourist actions underwater, suggesting that descriptive norms (perceived behaviors of others) and injunctive norms (perceived behaviors that are socially approved) play crucial roles in shaping diver conduct. Finally, using random forest machine learning models, I further elucidate the factors influencing reef contacts, emphasizing the significant impacts of concurrent tourist behaviors, wildlife sightings, tour operator eco-certification, and accessory use (e.g., cameras, gloves). Eco-certification schemes, such as Green Fins, can mitigate

intentional reef contacts, but they do not universally reduce overall reef impacts, necessitating nuanced and complementary approaches to improve their overall effectiveness. The chapter concludes with actionable recommendations for adaptive and socio-ecologically integrated conservation management strategies. These include refining dive certification processes to enhance reef conservation awareness, implementing stricter regulations on accessory use, and leveraging social norms to promote responsible diving behaviors.

7.2: Integrated Insights

The findings across these chapters reveal a consistent theme: the complex interplay between human behavior, biodiversity, and conservation policy at multiple scales—from the micro-level of individual consumer choices and tourist behaviors to the macro-level of global trade and regulatory frameworks.

At the macro scale, Chapters 2, 3, and 4 illustrate how large-scale economic systems (e.g., wet markets, online wildlife trade, and tourism industries) impact environmental health. In each case, challenges are compounded by intricate cultural, economic, and ecological tradeoffs, where tailored regulatory strategies are essential to address biodiversity and public health concerns without undermining local livelihoods or cultural practices.

At the micro scale, Chapters 3 and 6 emphasize the pivotal role of individual behaviors—whether through consumer choices in the ornamental fish trade or tourist actions on coral reefs. Both chapters highlight the gap between intentions and impacts, underscoring the need for behavior change interventions that are not only effective and efficient but also enduring and equitable. This implies creating behavioral shifts that benefit both nature and human well-being, while respecting social and economic realities.

Together, these chapters demonstrate that conservation policies must operate across institutional levels—local, national, and international—and geographical scales, balancing human activity with the needs of biodiversity. To address these interconnected challenges, conservation strategies must integrate innovative, data-driven interdisciplinary science, combining ecological data with behavioral insights to design interventions that achieve long-lasting and widespread change.

Moreover, my dissertation identifies significant data gaps in the wildlife trade and reef tourism sectors and proposes novel methodological approaches, such as the use of web-scraping techniques and machine learning, to close these gaps. My research further argues for an integrative focus on tailored regulation, recognizing the existence of double or triple tradeoffs faced by policymakers—balancing ecological sustainability with economic development and social equity.

Through this macro-micro lens, my dissertation ties together the larger themes of biodiversity conservation and human-nature interactions. My dissertation title, *Nature vs. Human Nature*, reflects the central ethical tension: the frequent misalignment between what is good for nature and what is good for humans. In contexts where human activity threatens ecosystems, I call for policies that acknowledge both the intrinsic value of biodiversity and the practical needs of human societies. I emphasize the need to design interventions that mitigate conflicts and create win-win scenarios whenever possible. And, I highlight the importance of recognizing both the systemic impacts of human activities and the need for targeted, context-specific interventions that can reconcile the often-contradictory demands of ecosystem conservation and human well-being.

7.3: Next Steps

The findings and methodologies developed in my dissertation offer numerous pathways for future research and policy interventions. One of the primary insights is the need for more refined and tailored regulation, recognizing the complex trade-offs policymakers face in balancing public health, food security, economic needs, and biodiversity conservation. To address these multifaceted challenges, future research should integrate behavioral science, ecology, and policy studies, designing interventions that account for both socio-ecological complexities and the bounded rationality of human behavior.

At the macro level, expanding upon the regional analysis in Chapter 4, a global study of coral reefs could examine the various anthropogenic stressors they face and the ecosystem services they provide. This approach, built on high-resolution mapping techniques and socio-ecological data, would allow for the identification of global hotspots of coral reef degradation and areas of exceptional resilience. A socio-ecological model could be developed to identify the key drivers behind reef health and to target conservation efforts at "overperforming" reef systems, helping prioritize interventions where they are most needed.

Simultaneously, further research should address the data gaps identified throughout the dissertation, particularly in the ornamental fish trade and reef tourism. Many species traded online remain unrepresented in global biodiversity databases, reflecting the broader challenges of data collection and biodiversity tracking. The methodological innovations proposed—combining web-scraped data with conservation databases—could serve as a blueprint for future biodiversity studies. Additionally, the primary observational and survey data from

Chapter 6 offers a promising model for investigating human-nature interactions across a broader array of ecosystems and anthropogenic stressors.

Unspoken but imperative, I also call for a comprehensive conservation policy framework that respects both the intrinsic value of biodiversity and the practical realities of human needs. The tension between these two imperatives highlights the ongoing challenge of aligning human activities with ecological preservation. Conservation efforts must not only respond to immediate threats but also recognize the long-term stakes, bridging the gap between biospheric values and practical governance.

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