Master's thesis

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A Global Model for Marine Invasive Species Distribution via Plastic Debris

Master's thesis in Industrial Ecology
Supervisor: Francesca Verones
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Abstract

Marine ecosystems are threatened by the proliferation of invasive species through resource competition, habitat modification, and disease transmission. These factors can accelerate the decline of native species and disrupt ecosystem dynamics, negatively impacting biodiversity and the services these ecosystems provide. One emerging pathway for the spread of marine invasive species is through colonization, or rafting, on plastic debris. Plastic items like bottles, bags, and fishing gear can serve as transportation vessels, enabling marine species to traverse great distances and establish themselves in foreign ecosystems. Here, we propose the inclusion of a novel impact category in Life Cycle Impact Assessment (LCIA) focused on the biodiversity impacts of marine invasive species introduced via rafting. This impact category will incorporate an existing fate model for the proliferation of ocean plastic, as well as an effect model which assesses biodiversity impacts of introduced species. In our research, we develop a model which functions as an exposure factor within this impact category, assessing the dispersal of alien species as a result of ocean plastic proliferation. Furthermore, this model allows us to identify and map global hotspots for invasion risks from rafting. Our work represents a truly novel combination of ecological theory and industrial ecology methods, drawing heavily on both island biogeography and modern analysis tools. In this paper, we present a case study on the implementation of our model, looking at alien species proliferation in the South China Sea. Globalization of this model and integration within LCIA will enable more comprehensive assessment of the environmental consequences of human activities on marine biodiversity.

Sammendrag

Marine økosystemer trues av spredningen av fremmede arter gjennom konkurranse om ressurser, endring av habitat og overføring av sykdommer. Disse faktorene kan akselerere nedgangen til innfødte arter og forstyrre økosystemers dynamikk, med negative konsekvenser for biologisk mangfold og tjenestene disse økosystemene gir samfunnet. En ny framvei for spredning av marine fremmede arter er kolonisering, eller flåting, på plastavfall. Plastgjenstander som flasker, poser og fiskeredskaper kan fungere som transportmidler som gjør det mulig for marine arter å krysse store avstander og etablere seg i fremmede økosystemer. Her foreslår vi inkluderingen av en ny påvirkningskategori i Life Cycle Impact Assessment (LCIA) som fokuserer på de biologiske konsekvensene av marine fremmede arter introdusert gjennom flåting. Denne påvirkningskategorien vil inkorporere en eksisterende modell for spredning av havplast, samt en effektmodell som vurderer konsekvensene for biologisk mangfold av introduserte arter. I vår forskning utvikler vi en modell som fungerer som en eksponeringsfaktor innenfor denne påvirkningskategorien, og evaluerer spredningen av fremmede arter som et resultat av økningen i havplast. Videre gjør denne modellen det mulig for oss å identifisere og kartlegge globale hotspots for invasjonsrisiko fra flåting. Vårt arbeid representerer en helt ny kombinasjon av økologisk teori og metoder innen industriell økologi, og bygger tungt på både øybiogeografi og moderne analyseverktøy. I denne artikkelen presenterer vi en case-studie om implementeringen av vår modell, der vi ser på spredningen av fremmede arter i Sør-Kinahavet. Globaliseringen av denne modellen og integrasjonen i LCIA vil muliggjøre en mer omfattende vurdering av de miljømessige konsekvensene av menneskelige aktiviteter for marine biodiversitet.

Acknowledgements

"There lies the port; the vessel puffs her sail:

There gloom the dark, broad seas."

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1 Introduction

1.1 Invasive Species

1.1.1 What are Invasive Species?

Invasive alien species (IAS) are one of leading drivers of global biodiversity loss (Bellard et al., 2016). Non-native organisms in any ecosystem are referred to as alien species, and such species are classified as invasive when they "negatively impact native biodiversity, ecosystem services or human economy and well-being." (IUCN, 2022). Since the Pleistocene, human activity has negatively impacted ecosystem quality through overexploitation, and more recently, habitat degradation and pollution (Ceballos et al., 2015). However, the widespread proliferation of alien species is a much more recent phenomenon (Figure 1). The 20th and 21st centuries have seen globalization link many previously disconnected regions of the world, and in the process, link many of its ecosystems as well. In this way, transportation and commerce have inadvertently carried many of the world's species into previously inaccessible habitats (Pysek et al., 2020). This has been further exacerbated by intentional introductions of alien species, for both aesthetic and industrial purposes (Carpio et al., 2016). These anthropogenic forces have, together, contributed to the increasing proliferation of alien species in recent decades.
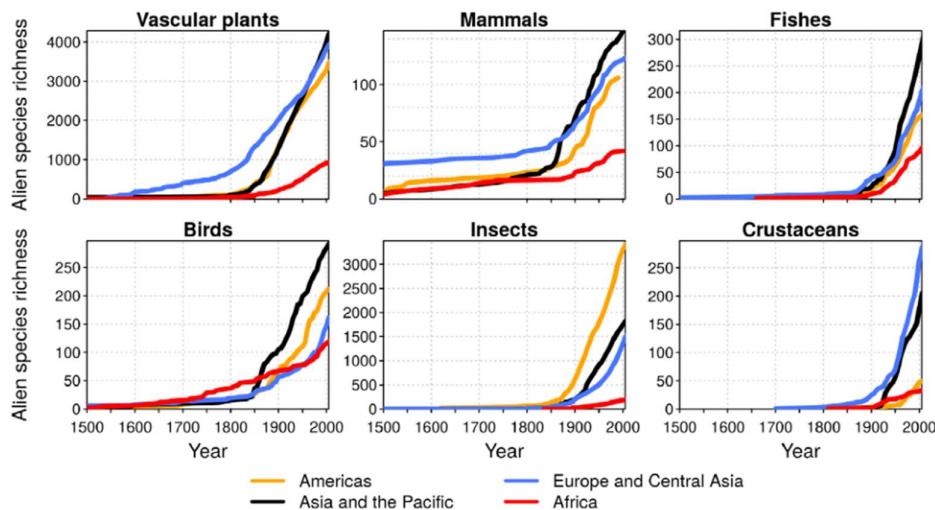
Figure 1: *Historical proliferation of alien species richness of multiple taxa across regions. Note the substantial increase in most taxa since 1900. Historically linked regions (Europe, Asia) exhibit earlier increases in invasive species. "Time series are based on the year of first record of those alien species that later became established in the given region." Source: Pysek et al., 2020.*

Invasive alien species (IAS) are characterized by their ability to rapidly spread and establish self-sustaining populations in new environments. The impacts of invasive alien species on ecosystems can be far-reaching and detrimental. Primarily, they have led to the displacement or extinction of native species through competition for finite resources (e.g., habitat and nutrients) and predation of existing species (Clavero et al., 2009) (Courchamp et al., 2007). IAS may also introduce new diseases or parasites, alter nutrient cycling, or more broadly impact ecosystem function (Molnar et al., 2008). The consequences of invasive alien species extend beyond the realm of ecosystems, affecting human industries such as agriculture, forestry, and fisheries; economic losses reach millions of dollars each year in the US, on top of human health and cultural value losses tied to healthy ecosystems (OTA, 1993) (Vitousek et al., 1997). Globally, about 37% of historically alien species have become successfully established, and while not all of these are invasive, this number represents significant ecological impacts (Pysek et al., 2020) (Figure 2). However, the impacts of IAS are not evenly distributed: many of the most heavily impacted ecosystems are islands, such as New Zealand and Hawaii, with high endemism and limited migration (Pysek et al., 2020). This highlights the need for assessing the specific mechanisms involved in the spread of IAS. Efforts to prevent the introduction and control the spread of invasive alien species are crucial for preserving the integrity and resilience of ecosystems worldwide.
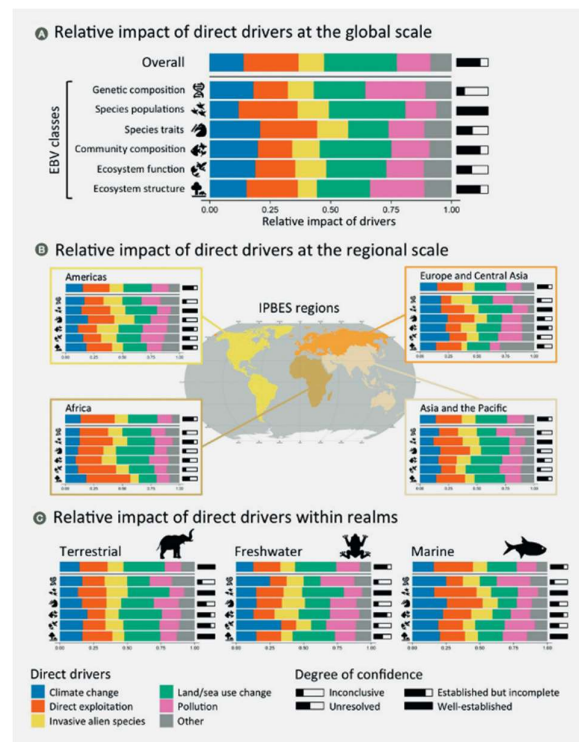
Figure 2: "*Relative impact of direct anthropogenic drivers (color bars) on the state of nature at the global scale (A), within each IPBES region (B) and for terrestrial, freshwater and marine realms (C)." Confidence interval is included next to each taxon. Note the yellow bars for each category, representing the relative significance of invasive species in impacts. Source: IPBES.*

1.1.2 Management Challenges

Managing the challenges posed by IAS has become an increasingly daunting task for the conservation community. Although the potential impact of IAS is well understood, determining the true extent of their effects in practice can often be challenging. Paradoxically, the introduction of alien species often results in an overall increase in species richness within the introduced regions (Thomas, 2013). However, it is important to recognize that an increase in richness in the short term does not always translate to positive outcomes for ecosystems in the long term (Valiente-Banuet et al., 2015). In many instances, the presence of IAS leads to a significant reduction in the distribution of native species, even though it may not drive them to extinction (Pysek et al., 2020). Consequently, IAS can profoundly alter the structure and functioning of local ecosystems, although their impacts may appear inconspicuous depending on the specific indicators used to assess them (Thomson, 2020). The negative consequences of IAS often occur in conjunction with other threats to native species, such as habitat loss. As a result, it can be more straightforward to attribute the observed impacts to conspicuous drivers like deforestation, rather than recognizing the hidden mechanisms underlying the influence of IAS (Harfoot et al., 2021).

Containing the spread of invasive alien species (IAS) poses an immense challenge as well. Alien species can infiltrate novel ecosystems through both marine and terrestrial pathways, such as shipping, tourism, and common transport (Pysek et al., 2020). Safeguarding against alien species spread in each of these pathways necessitates a high level of diligence across many economic sectors. One example of successful IAS management is the eradication of the black-striped mussel (*Mytilopsis*) in Australia. The success of this operation hinged upon early detection, rapid mobilization, and comprehensive eradication strategies (Myers et al., 2000). Moreover, once alien species establish themselves in an ecosystem, eradicating them becomes an even costlier endeavor. For example, in 2006, the US federal government allocated a budget of 1.3 billion USD to invasive species management (Mehta et al., 2007). Consequently, from both economic and conservation standpoints, the implementation of effective early detection and management strategies is crucial for averting the most severe impacts of IAS (Pearson et al., 2021).

1.2   Marine Invasive Species

1.2.1 A Growing Threat

IAS are not only a growing threat to terrestrial ecosystems, but marine ecosystems as well. In fact, due to ecosystem interconnection and inaccessibility, marine ecosystems can be even more challenging to manage (Giakoumi et al., 2019). In addition, research on marine IAS has consistently lagged behind that of terrestrial species (Davis, 2009). As a result of the expansion of shipping, aquaculture, and more recently, anthropogenic debris like plastic, globalization has exacerbated the threat to marine IAS as well (Garcia-Gomez et al., 2021). As of 2008, only 16% of maritime ecoregions are thought to be free from alien species (Figure 1), and the number of such incursions has likely increased since (Molnar et al., 2008).
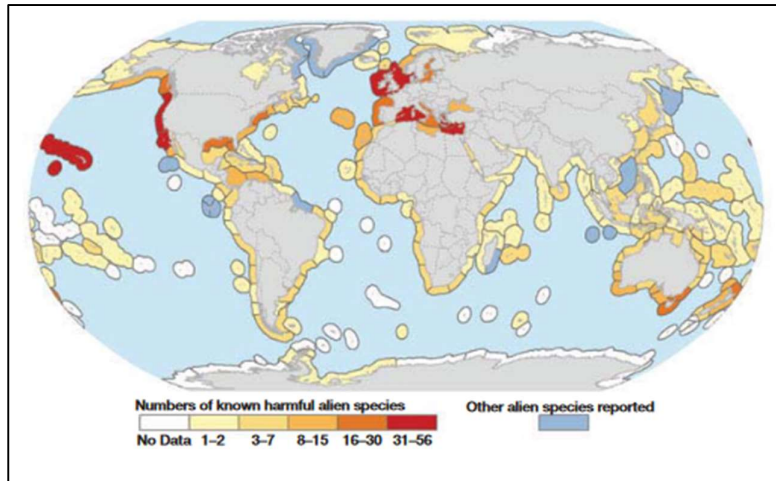
Figure 3: *Documented alien species with high ecological impact scores (3 or 4), by marine ecoregion, with darker shades indicating a greater number of species. Ecoregions in which only less harmful species have been observed are colored blue. Adapted from Molnar et al., 2008.*

Marine shipping introduces IAS into novel marine ecosystems via hull fouling and ballast water. 'Hull fouling' denotes the process of direct attachment of marine species to the hulls of shipping vessels, from which they can reproduce directly into the surrounding ocean. Marine species can also be drawn into a ship's ballast water in one ecosystem, transported across shipping routes, and then released in another ecosystem as the ballast water is exchanged again in port (Lo et al., 2012). According to Molnar et al. (2008), these methods of dissemination are the primary means of transporting marine IAS. However, more recent International Maritime Organization (IMO) regulations regarding the exchange of ballast water have probably reduced many of the worst impacts of marine IAS from shipping (IMO, 2022). After shipping, aquaculture represents the second-largest vector of marine IAS dispersal (Molnar et al., 2008). This mechanism is primarily driven by accidental, localized introductions of marine species raised for consumption. One striking example is the *Crassostrea gigas* oyster, which was originally grown in aquaculture throughout much of coastal Europe, but since escaping has decimated biodiversity in the Mediterranean (Ruesink et al., 2005). Even from the confines of aquaculture, however, any parasites that such species may possess have the potential to wreak havoc on local ecosystems and further endanger native species (Naylor et al., 2001). Together, these vectors represent the primary historical drivers of IAS in marine ecosystems.

Much of the research surrounding marine IAS has been devoted to studying the risks of invasion via aquaculture and shipping, but much less has focused on the risks of IAS spread by anthropogenic debris (Garcia-Gomez et al., 2021). Natural debris has historically been an important means of transoceanic migration for both marine and terrestrial organisms (Barnes and Milner, 2005). Such 'rafting' is a method of dispersion that is particularly valuable for sessile marine species, whose life cycles do not involve a pelagic stage. In fact, immigration via rafting has always served as one of the most significant evolutionary forces in the remote ecosystems of the earth (Thiel and Gutow, 2005). In recent decades,

however, the proliferation of floating anthropogenic debris has greatly accelerated the rate of transoceanic immigration. Field surveys suggest that anthropogenic debris has more than doubled the chances of IAS dispersal across tropical marine environments (Barnes, 2002). While such studies are clearly valuable, the lack of widespread data on this subject means that the most significant routes of IAS transport on debris are still not clear (Molnar et al., 2008). Textiles, wood, and buoyant metals are just a few examples of anthropogenic trash that persist on the ocean surface, and thus act as vectors of species dispersal (Ibabe et al., 2020). However, of all the anthropogenic substrates, plastic debris in particular has gained increasing attention from the conservation community as a vector for rafting.

1.2.2 The Plastic Problem

Between 1950 and 2017, the total amount of plastic produced worldwide has increased from 0.5 to 348 million tons (Audrezet et al., 2021). Such enormous production volumes have turned plastic into one of humanity's most pervasive sources of pollution. Approximately 10% of the world's plastic waste finds its way into the oceans, which constitutes roughly 61 to 87% of the anthropogenic debris currently present in marine ecosystems (Garcia-Gomez et al., 2020). The presence of so much plastic in the oceans profoundly impacts marine life through several mechanisms, including the entanglement of large marine animals by macroplastics and the pollution of food webs by microplastics (Audrezet et al., 2021). These plastic impacts are well-known, indisputable, and addressing them is crucial for ocean conservation efforts moving forward. However, a different, increasingly visible impact of ocean plastic problem is its role in the dispersal of IAS, due to its persistence within ecosystems and its potential for extensive spatial mobility.

The true impact of IAS from plastic debris has likely been underestimated in the field of invasion ecology thus far (Garcia-Gomez et al., 2020). Field surveys have documented numerous instances of marine species using plastic debris as rafts for dispersal, and in many cases, a significant portion of these species are not native to local ecosystems (Carlton et al., 2017) (Barnes and Fraser, 2003). The dispersal potential of organisms on plastic rafts is theoretically constrained by both biotic factors, such as the availability of prey, and abiotic factors, such as ocean temperature. For instance, native Mediterranean species may face substantial challenges surviving a transatlantic journey that ends on the shores of northern Canada. However, field studies have repeatedly demonstrated the remarkable persistence of rafting species, even in the frigid oceans of Antarctica (Barnes and Fraser, 2003). Plastic debris possesses remarkably long lifespans, resisting natural decomposition processes over thousands of years. Moreover, plastic is incredibly buoyant, allowing debris to remain afloat for extended periods of time, thus facilitating the transport of alien species across vast spatial scales (Audrezet et al., 2021). Compounding the problem further, laboratory studies have demonstrated that some common marine larvae exhibit a preference for plastic as a substrate over other substrates (Pinochet et al., 2019). Consequently, as the volume of ocean plastic continues to rise, plastic debris represents an emerging pathway for the introduction of IAS that demands increased attention in the coming years.

1.3 Modelling Marine Invasive Species

1.3.1 Existing Research and Global Relevance

Although field data on plastic rafting remains somewhat limited in quantity and scope, attempts to develop a global understanding of its impacts are nonetheless valuable (Garcia-Gomez et al., 2021). IAS pose a global challenge, as their proliferation stems from transnational human activity, and their effects are most pronounced in distant ecosystems (Molnar et al., 2008). And, regarding rafting specifically, it appears evident that the distance traveled by a plastic object does not significantly affect the survival of resident species (Barnes and Fraser, 2003). Therefore, even though globalized rafting models may rely on a limited pool of field data, they are indispensable for assessing the scale and potential impact of marine IAS. Field studies can play a crucial role in constructing accurate models, while models can provide the framework for interpreting localized observations.

At present, marine IAS models are largely limited to the dispersal of marine invasive species through shipping routes (Seebens et al., 2017). However, to our knowledge, there are no existing models aimed at characterizing the flow of marine alien species via debris. Several factors contribute to this knowledge gap: a) the true fate of ocean plastic is still quite poorly understood (Audrezet et al., 2021); b) modeling the complex interplay of ocean currents and wind patterns presents a unique challenge on its own, though recent work in this field has contributed substantially to our understanding of ocean current dynamics (Hoiberg, in preparation); c) few laboratory experiments have been conducted to explore the physiological aspects of species attachment to rafts, and the conditions under which this occurs; and d) predicting the immigration and survival rates of rafting species poses a significant challenge (Thiel and Gutow, 2005). Furthermore, the wide array of plastic debris types, each with distinct drift behaviors, physiochemical characteristics, and resident taxa compositions, further complicates the development of global models (Ibabe et al., 2020). Of course, plastic has only recently been recognized as a potential carrier of invasive species, hence the scarcity of research in this particular domain (Garcia-Gomez et al., 2021). Despite these limitations, the utilization of large-scale IAS models can serve as a catalyst for increased localized field studies and research efforts. In this way, such models serve a valuable purpose in furthering our understanding of invasion ecology and conservation.

1.3.2 LCA as a Tool for IAS Impact Analysis

Life Cycle Assessment (LCA) is a tool for evaluating the environmental consequences associated with specific industrial activities (Muralikrishna and Manickam, 2017). Based on personalized inventory data, LCA creates a comprehensive assessment of environmental impacts across the entire life cycle of a product or process, encompassing its production, use, and end-of-life stages. These impacts are quantified relative to a functional unit, employing characterization factors specific to each impact category, thereby providing a quantified measure of impact per unit of activity. For instance, when conducting an LCA of the aquaculture industry in Norway, one may attempt to calculate the potentially disappeared fraction (PDF) of marine species per kilogram of salmon consumed by an individual. This robust tool facilitates the quantification of humanity's environmental

footprint by comparing the boons and banes associated with different products or processes, effectively pinpointing the most impactful aspects within their value chains (Hauschild and Huijbregts, 2015).

Life Cycle Impact Assessment (LCIA) is the specific component of LCAs focused on calculating and aggregating environmental impacts. LCIA involves taking the quantities of environmental stressors generated by the process under study, then using Characterization Factors (CFs) to convert these quantities into impacts. CFs typically consist of multiple intermediate factors that describe the dispersion and ultimate impact of the given environmental stressors. These factors consist of:

- a Fate Factor (FF), which describes the distribution of a stressor within environmental compartments (e.g., how effectively a pesticide spreads from soil to rivers, and within the river)

- an Exposure Factor (XF), which describes how effectively the stressor passes from these geographically defined compartments into biotic systems (this accounts for the fact that not all pollutant is bioavailable/pervades ecosystems)

- and an Effect Factor (EF), which describes how the presence of the stressor affects members of a local population

These factors are multiplied together to produce a CF (Equation 1), allowing LCA practitioners to calculate the environmental impacts from a range of emitted stressors (Wilson, 2022) (Hauschild and Huijbregts, 2015).

$$(1) \qquad CF = FF * XF * EF$$

There is a growing body of research dedicated to refining LCIA methodologies, expanding the range of impacts considered, and improving the estimation of existing impacts (e.g., regionalization) (Bare, 2010). Enhancing the accuracy of impact quantification enhances the relevance of assessment outcomes. In the context of invasion ecology, for example, LCIA methodologies can be employed to quantify the proliferation and impact of invasive species resulting from specific industrial activities—a valuable tool for preempting invasion risks.

In this paper, we contribute to this expanding body of LCIA research by incorporating the biodiversity impacts from the spread of marine alien species via plastic rafting. This particular impact category has never before been included in LCIA methodologies. Ongoing projects integrating marine biodiversity impacts into the LCA framework are focused on modeling the global flow of plastic throughout ocean ecosystems (Høiberg et al., in preparation), and quantifying the impacts of alien species following their introduction to marine ecosystems (Gjedde et al., in preparation). These two models will serve as the Fate Factors FF and EF, respectively, within our novel impact category. Building upon these projects, our model seeks to establish a connection between ocean plastic flows and the

impacts of alien marine species. Consequently, the model will be implemented as an XF within LCIA, acting as the link between the proliferation of industrial substances and biotic systems, providing a more comprehensive description of the marine biodiversity impacts of human activities. Additionally, our model will enable the identification of global hotspots for alien species introduced via plastic rafting. Thus, our model will be incorporated within this new impact category in LCIA and can also be utilized independently as a tool for policymakers. Here, we present a single case study of our model, analyzing the proliferation of alien species from a single plastic release point in the South China Sea.

Parts of introduction modified from that of my own fall master's project (Wilson, 2022).

2 Methods

2.1   Model Framework

2.1.1 Data Sources

This model is statistical by nature, and does not attempt to describe real historical flows, or predict future flows, of specific invasive species. The theoretical framework for this model is based largely on the principles of island biogeography (MacArthur and Wilson, 1963). Much of the data that supports our calculations is drawn from existing studies of rafting ecology (see section 2.3). The dynamic flow of debris objects used in our model was derived from a separate fate model for the potential distribution of ocean plastic debris from Høiberg et al. (in preparation), which utilizes OceanParcels for Lagrangian particle tracking simulations (Lange and van Sebille, 2017). The fate model functions on a scale of these "ocean parcels", which are essentially pixelated ocean areas that simulate the potential distribution of plastic after a release from a given point in space. Our alien species model, however, relies on marine ecoregions as the basic level of functionality. These 'ecoregions' are a classification scheme for coastal and benthic shelf ecosystems developed by Spalding et al., (2007). Their borders are drawn based on geopolitical boundaries, ecosystem contiguity, and existing threats to resident marine species. There are 232 distinct ecoregions, which together cover the entirety of the world's coastline (Figure 4). There are a few reasons why this resolution is used here: first, it allows us to utilize the MarInvaders database (see section 3.2), which aggregates known species ranges from several existing databases, at the level of marine ecoregions, for both native and alien species (Lonka et al., 2021). The ecoregion scale also allows us to draw from 'source populations', as necessitated by the equilibrium theory of island biogeography (see section of 2.1.2). Finally, it allows us to aggregate ecological impacts within specific regions of the world, which can be more easily translated into country-level impacts in LCIA. Together, with these tools, data sources, and ecological concepts, we simulate the flow of species on plastic objects through marine ecoregions, then estimate the dispersal of alien species as a result of each individual flow.

Figure 4: *Marine Ecoregions of the World, created by Spalding et al., (2007). Each ecoregion is represented as a color distinct from its neighbors. Shapefiles acquired via databasin.org.*

2.1.2 Equilibrium Theory of Island Biogeography

Much of the model described herein is dependent on the theoretical framework known as the Equilibrium Theory of Island Biogeography (ETIB). This theory was originally described by MacArthur and Wilson in their landmark 1963 paper titled "An Equilibrium Theory of Insular Zoogeography". This ingenious ecological framework was used to describe the population dynamics of species living on remote islands. Using only a few crucial parameters, these equations could predict the species richness, immigration rate, and extinction rates of such islands (Figure 5). Later field studies demonstrated the remarkable accuracy of these predictions in real island ecosystems, including one highly controlled study conducted by Simberloff and Wilson that included removing entire insect populations from a few islands in the Gulf of Mexico, then recording the subsequent succession of species on the islands over a period of years (Simberloff and Wilson, 1969). It was not only MacArthur and Wilson who propelled the theory forward; rather, their work opened up a rich new subfield in ecology focused on island biogeography (Warren et al., 2015). This included critical work by Jared Diamond, which served to provide a stronger mathematical underpinning to the existing model. There are some limitations to field studies involving the ETIB. Primarily, it is incredibly difficult to establish evidence for an immigration-extinction equilibrium at a given moment in time (see Figure 5). Further, while an equilibrium of species richness may become established on a given island, this equilibrium can change over time as a result of species interactions and niche optimization (i.e., succession) (Warren et al., 2015). Nonetheless, the field studies that do exist have proven robust enough to ensure the continued use of the ETIB in ecological models today.

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Since the inception of the ETIB in 1963, the theory has shown to have a wide range of applications in ecology beyond island biogeography. For example, it has been used in the field of Conservation Biology to describe population dynamics in habitats fragmented by human activity (habitat fragments act as 'islands', with their own unique rates of immigration and extinction), providing valuable insight into the risks of local extinction (Diamond, 1973). In addition, the species-area relationships used in LCIA to create species-sensitivity distributions are themselves closely linked to ETIB (Lomolino, 2000). Since the first description of evolution by Charles Darwin, islands have served as valuable model systems for ecology and evolutionary biology, and continue to provide insights and applications in these fields today (Warren et al., 2015).
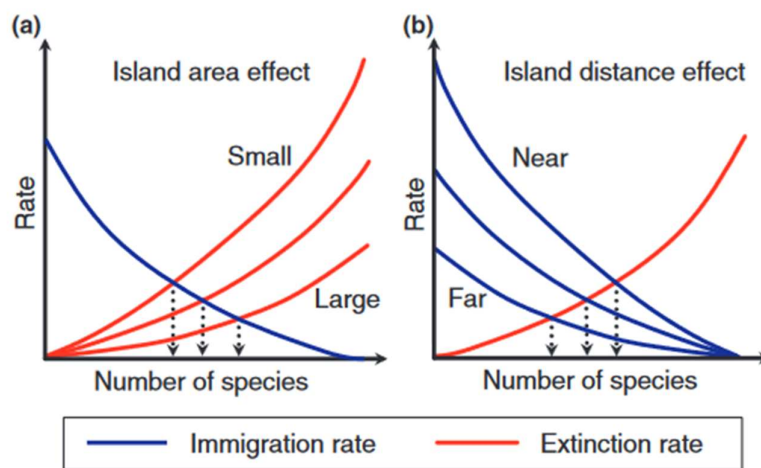
Figure 5: *Graphical representation of the equilibrium theory of island biogeography. "The Core IBT model, illustrating MacArthur & Wilson's (1963, 1967) assumptions regarding the following: (a) the effect of island area on extinction rate, and (b) the effect of distance from the mainland on immigration rate. Predicted species numbers appear on the x-axis, with dotted arrows marking equilibria between immigration and extinction rates." From Warren et al., 2015.*

The ETIB forms the foundation of the model presented here. In many ways, the flow of species on and off drifting plastic debris resembles the population dynamics of islands. To start with, the species composition of any given plastic item is dictated by the immigration and establishment of species from the surrounding ocean on the plastic item. Further, each plastic item possesses its own unique community of marine species, with its own species interactions, ecologies, and extinction rates, in the same way that every island is distinct from another. Much of this difference is a result of probabilities, in the sense that immigration is an inherently probabilistic phenomenon (it is not guaranteed that every species which immigrates establishes itself in a novel habitat). In the same way, this model is inherently probabilistic in terms of each raft's species richness. Additionally, the use of marine ecoregions as the functional scale of this model means that we can practically establish a 'source population', or a 'mainland', from which a specific batch of species can

feasibly emigrate to each rafting item. The marine ecoregion that any given plastic item is in represents the 'mainland', and the plastic items themselves represent the 'islands'. In the marine realm, however, immigration dynamics of source populations are more complicated than true islands, due to the lack of a physical immigration barrier. Water is the only substrate in which species travel through marine ecosystems, and it is interconnected throughout the world's oceans. However, the nature of rafting ecology dictates that most species attached to plastic objects are mostly seafloor- or substrate-dependent species (Thiel and Gutow, 2005). Thus, the water itself does, in a sense, act as a physical 'barrier' to immigration, and the distance between the plastic item and the seafloor (i.e., ocean depth) can serve as the distance between the 'mainland' population and the 'island' ecosystem. Finally, in the ETIB, the size of each island is an important parameter in determining its carrying capacity, and thus its equilibrium species richness. In the same way, the size of a rafting object greatly determines its own species richness, depending on the distance it has already traveled (Carlton et al., 2017). Though we neglect it in our model (see section 2.2.2), raft size-based variations in species richness further support the translatability of the ETIB into the field of rafting ecology.

The mathematical foundation for our model equations is drawn largely from Gilpin and Diamond's (1976) seminal work on ETIB models of Salomon Island bird dispersal. In Gilpin and Diamond's paper, they attempt to explain observed population dynamics of Salomon Island bird species using the ETIB. Specifically, they formulate a range of different equations based on the ETIB model, and they fit these various mathematical models with their own field data to find the most biologically accurate model of island biogeography. While this paper is indeed old, to our knowledge, there has been no other biogeographical research that so comprehensively translates robust field data into mathematical representations of the ETIB. Critically, Gilpin and Diamond also discuss the translatability of these equations to other applications of the ETIB, and where species-specific changes should be made depending on the context. Critical differences between Pacific Island ecosystems and the raft ecosystem are discussed further throughout sections 2.2 and 2.3 and are subsequently reflected in the construction of the equations presented herein. Ultimately, Gilpin and Diamond present a single set of immigration-extinction equations that most accurately fit their field data (explains 97% of variance), while limiting the number of parameters required to 3 (i.e., parameters specific to each island). These equations are presented in section 2.2.

2.1.3 OceanParcels Fate Model & Connection to Alien Species Model

For the alien species model to function as intended, it requires a simulation of plastic drift throughout the world's oceans, upon which species can raft. For that, we rely heavily on Høiberg et al.'s (in preparation) ocean plastic fate model: a novel application of OceanParcels, a Lagrangian particle tracking model (Lange and Sebille, 2017). For a given piece of plastic residing in an ocean parcel pixel, there is a certain probability assigned to each direction that the plastic particle enters the neighboring pixel. These probabilities are based on historical ocean currents and wind patterns, which together determine the flow patterns of plastic objects at sea. When aggregated together over a larger time scale, these pixel-to-pixel movements can paint detailed pictures of ocean surface plastic flows. The model can simulate the flow of plastic starting from any location in the world's oceans. It then stores information about the coordinates, time scale (about 1 'observation' every 6

hours), marine ecoregion, sovereign territory, and latitudinal zone of every plastic object simulated as it moves through the oceans. It also includes a stochastic 'disappearance' rate, which simulates the sinking of plastic particles that can occur during ocean drift (note: the fate model simulates what they call plastic 'particles', which we describe in our model as 'rafts'. For the purposes of this work, these two terms are used interchangeably to describe floating ocean plastic). Using these model outputs, we added unique species flows to each plastic particle, then estimated the impacts resulting from the movement of these particles into new ecoregions.

For testing the implementation of our alien species model, we ran a single simulation of 50 plastic particles in the OceanParcels model. In this simulation, we used the following input parameters: a total simulated flow time of 8 years (similar to the Japanese Tsunami debris data discussed in section 2.3.2); a difference of 6 hours between observations; a total release time of 1 year (i.e., all particles released over the course of a year, to account for seasonal variation in ocean currents); a total number of 50 plastic particles released, each of which were tracked in the alien species model; a central release point at 116.1525 deg E and 21.7635 deg N, the coordinates of the centroid of the 'South China' marine ecoregion; and a particle release radius of 50 km around the central release point. This ecoregion was selected because a) it is surrounded by four other ecoregions, allowing us to test our alien species model through as many ecoregions as possible, b) it is relatively small, ensuring that the plastic particles do not get trapped in the start ecoregion for a long period of time, and c) there is a high degree of commercial fishing that occurs in the South China Sea, and given the prevalence of fishing gear in ocean plastic (Morales-Casellas et al., 2021), it represents a realistic release point for plastic debris. This model, along with the species flow equations discussed in the following sections, allows us to quantify the flow of alien species on each of these 50 plastic particles over the course of 8 years.

2.1.4 Alien Species Model Functionality

Within a single ecoregion, our model works as follows: Based on the movement patterns of each plastic object, as well as the ecological characteristics of the ecoregion, we calculate the probability that a) some species inhabiting that ecoregion become a part of the raft community (i.e., attach directly to the raft, or otherwise begin relying on the raft community for nutrients); and b) some species in the existing rafting community 'unraft' from the object. When the raft moves into a new ecoregion, the calculations are repeated (Figure 6). Realistically, it is quite uncommon for rafting species to physically detach themselves from their inhabited substrate. More often, 'unrafting' represents species reproducing from the raft, and ejecting their propagules into to the surrounding ocean (Thiel and Gutow, 2005). As a result, this model does not remove 'unrafted' species from the existing raft community; their continued survival on the raft is instead limited by a death rate, or as we refer to it here, a local 'extinction rate'. Further, this model describes species richness (i.e., the number of species inhabiting each raft), not the abundance of individual organisms. This ensures compatibility with the effect factor developed by Gjedde et al. (in preparation). Finally, to make this model both regionalized and accurate, it relies on a wide range of ecoregion-specific parameters. The parameters used to simulate the mechanism described above are detailed in sections 2.2 and 2.3.
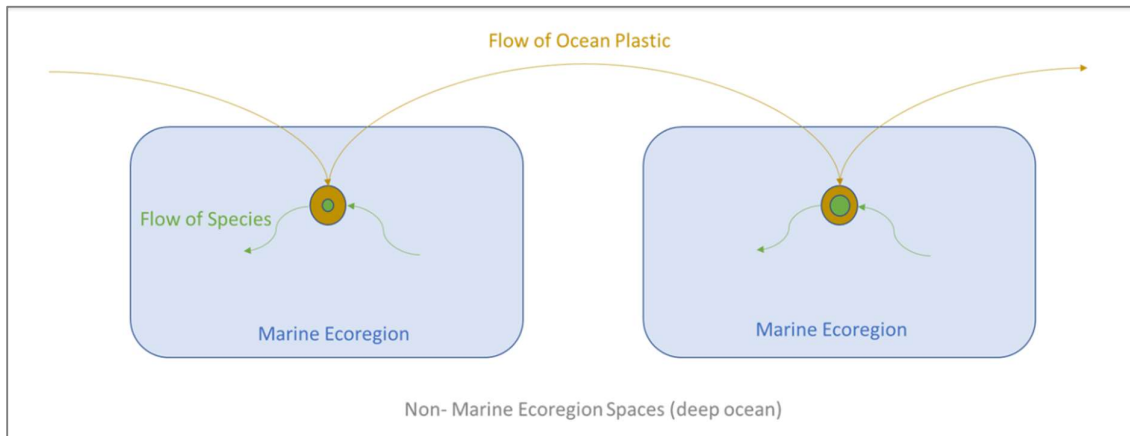
Figure 6: *Model Mechanism. Yellow lines represent the flow of plastic throughout the ocean. Blue shaded regions represent ecoregions. Green lines represent the flow of species between the raft and the ecoregion. As the raft moves between ecoregions, the number of rafting species increases.*

2.2 Construction of Model Equations

The equations implemented in this model to describe the flow of rafting species by ecoregion are detailed in this section. Gilpin and Diamond's (1976) biogeographical equations are used as the foundation for our own equations in this model. These equations are presented alongside our own for comparison, where applicable, shaded in light grey. Further discussion of differences between our model and theirs is included in section 3.2.6. Here, we broadly outline the construction of the four model equations, but further description of each of the equation parameters is included in section 2.3. A table listing all equation variables and their corresponding parameters is included at the end of this section. Finally, all supporting files for parameter calculations and model simulations are included in the appendix.

2.2.1 On-Rafting

Equation (2a) represents the number of species on-rafting in any given ecoregion, as a result of the flow of one plastic raft within that ecoregion. Equation (2b) represents Gilpin and Diamond's corresponding island immigration equation. In our model, the variable P_i represents the total number of species within the given ecoregion that have the ability to raft. In other words, it represents the source population from which immigrant species are drawn. It follows logically that the higher the source population, the higher the rate of immigration, due to a higher chance that some species somewhere on the mainland decides to make the journey across the abiotic barrier. In this sense, the source population size is an important parameter in the immigration component of island biogeography. c represents the number of species already living on the raft at any given point in time. In this equation, c_i is included in a ratio with P_0 and subtracted from 1, such that the closer the resident species number is to the source population size, the fewer species on-raft in

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each ecoregion. This is and set to the power of $2n$, which is a species-specific best-fit parameter described in Gilpin and Diamond's equations, varied according to the species or community currently being modelled. The variable x_i represents the plastic flow parameter, which describe the total distance a plastic particle has drifted through ecoregion i. Thus, the longer the distance each piece of plastic travels in an ecoregion, the higher the chances of on-rafting from local species. d is a value corresponding to the average depth of the given ecoregion. Each ecoregion has its own unique depth average, which is used as a proxy for the raft's distance from the ocean floor. In island biogeography, the distance from an immigration source is inversely related to the rate of immigration (Fattorini, 2009); in this case, species 'emigrate' to the raft from substrates on the ocean floor, so the distance they or their larvae must travel is an important component of their on-rafting probability. In our equation, the distance travelled by each plastic raft (x) stands in a negative ratio with the average ecoregion depth (d), contained within a base e exponential function. The exponential function here turns this ratio into a value between 0 and 1, and it serves to prevent a negative on-rafting result if the ecoregion depth (d) exceeds the distance travelled in the ecoregion (x). The final component of equation (2) is the derivative parameter, $\left(\frac{d}{dt} c_{\max t,i}\right) t$. This essentially allows us to calculate a maximum plausible number of on-rafting species per ecoregion, depending on the time the plastic particle has spent at sea. The previously discussed operations in this equation then serve to reduce the equation output to an on-rafting rate that is more specific, given the biophysical constraints of that ecoregion and the existing rafting community. Thus, the output of equation (2), in units of species, is the number of possible on-rafting species per ecoregion.

$$(2a) \qquad S_i^{on} = \left(1 - \frac{c_i}{P_i}\right)^{2n} \exp\left(-\frac{d_i}{x_i}\right)\left(\frac{d}{dt} c_{\max t,i}\right) t_i$$

$$(2b) \qquad I = \left(1 - \frac{S}{P_0}\right)^{2n} \exp\left(-\frac{\sqrt{D}}{D_0}\right)$$

As related to the ETIB, the on-rafting equation (Equation 2) represents the immigration rate of species to "islands". Compared to Gilpin Diamond's version of this equation (Equation 2b), we see some notable differences. The first operation in parentheses is exactly the same (their S is the same as our c), but the second operation is slightly different. Here, both models use an exponential function (base e), but Gilpin and Diamond use a square root of the distance, D, from mainland to island in a negative ratio with D_0, which represents the average dispersal distance of the species being modelled. This operation functions such that the higher the dispersal distance and the lower the island distance, the higher the immigration rate. However, we have exchanged the island distance D with ecoregion depth d, due to the corollary nature of these parameters, and we have removed the square root, due to the relatively small values that d represents. We have also exchanged the average dispersal D_o with x. This is primarily because, in ocean ecosystems, local migration is very weakly dependent on dispersal distance; in many cases, marine larva dispersal can occur on the scale of hundreds of kilometers, which more than encompasses the scale of a single ecoregion (Alvarez-Noriega et al., 2020). As a result, marine dispersal distances (D_0) can be thought of as infinitely large in an ecoregion-based model, and thus useless. However, unlike the classical ETIB model, these plastic

rafts spend only a limited amount of time as "islands" relative to each "mainland" ecoregion. Thus, the time spent in each ecoregion heavily influences the on-rafting probability in that ecoregion. However, in our model, we include both a distance component (x_i) and a time component contained within the $c_{\max t,i}$ parameter. This may seem like a sort of 'double counting', but the distinction between distance and time is crucial. Time is likely more important than distance in terms of how many species on-raft (more time per ecoregion means more time for species to on-raft). For example, if a raft travels a long distance in one ecoregion, but does so quickly, it will likely experience little on-rafting compared to a raft that travels a short distance over an extended period of time. However, a longer distance travelled also means exposure to a wider range of local ecosystems and rafting species, so distance is an important parameter on its own. The distance travelled parameter thus replaces Gilpin and Diamond's dispersal distance parameter (D_0), where its sensitivity is weak relative to the time component of the raft (see section 3.1.4). This also serves to conserve units across the two equations, a necessary component of our model's integration within LCIA.

$$(3) \qquad c_i = \sum_{i_0}^{i-1}(S^{on} - E)$$

Equation (3) describes our method used to calculate c for any given region. Essentially, in any given ecoregion, c_i is the sum of on-rafting species from all previous ecoregions the plastic raft has traveled through. Thus, when a raft crosses into a new ecoregion, the c value remains constant for the duration of its travel throughout the ecoregion; then, a new c value is calculated based on the on-rafting parameters for that ecoregion. We include this parameter because the establishment probability of an immigrant species is dependent on the community already established there. While there can be some exceptions to this rule (e.g., niche sorting), the more species there already are on an island, the harder it is for a new species to establish itself, due to predation, competition, and spatial pressure from existing species (MacArthur and Wilson, 1963). Thus, as the parameter c_i increases with ecoregion travel, the on-rafting probability decreases according to the remaining parameters in equation (2a).

2.2.2 Local Extinction

An extinction (E) equation is also included in this model, representing the extinction rate of rafted species in each encountered ecoregion (Equation 4a). As in island biogeography, there is an inherent probability that species in a confined ecosystem will go extinct due to competition/predation from other species, a statistic which is classically related to the island size and number of existing species. However, in our model, every raft particle has the same average area, which thus makes variations in surface area negligible. Thus, the extinction equation yields, in units of species, an extinction rate for rafting community in each ecoregion encountered. In a functional sense, in each ecoregion, a certain number of species will be randomly selected for extinction from the existing rafting community on each plastic raft. This parameter not only replicates real-world community dynamics, but also serves to introduce further stochasticity into the model.

(4a) $E_i = c_i\,(1 - r)$

(4b) $E = \dfrac{RS^n}{A}$

As Diamond and Gilpin's extinction equation shows (Equation 4b), there are some species-specific variables which can determine extinction rates. Their extinction equation includes island species count, S, in a power function to the degree n (note, the same n as in the immigration function). They describe their corresponding coefficient, R, as the ratio of E_0 to I_0, which are species-specific constants. This accounts for the fact that, at equilibrium, the population size on an island is only dependent on the relative rates of extinction and immigration, not their absolute values. Finally, A represents the island size that Gilpin and Diamond use in their model. However, in this model, both raft surface area (A in their equations) and the species-specific constants (R and n) are constant across all scenarios, as we assume a single plastic debris archetype and raft species assemblage. Thus, the equation itself can be reduced to a single constant based on the existing number of species, so a linear extinction rate was favored in the current model. Further discussion of this model choice can be found in section 3.2.6.

2.2.3 Off-Rafting

The off-rafting equation is ultimately what determines the impact of introduced species from plastic rafting in our model. In contrast to the immigration-extinction equations described above, the off-rafting equation (Equation 5) is constructed in a slightly different way, for a few important reasons: most critically, the ETIB does not include any mathematical framework for subsequent dispersal from islands (which is essentially the process of off-rafting described in this model). Further, the rafting community is unique in that there is an exchange of species within each ecoregion that is dependent on the existing rafting community. The dispersal of species from each raft is likely not dependent on spatial limitations in the same sense as the previous equations are; rather it is much more dependent on the ecological characteristics of both the rafting community and the incumbent ecoregion. Finally, the parameters that determine a species' off-rafting potential are not mathematically interrelated in the way that they are within the ETIB. For example, the suitability of a single species to the temperature of a novel ecoregion is unrelated to the seafloor depth, both of which are important factors in determining establishment probability (Droghini et al., 2020). Thus, the off-rafting parameters can be treated as separate factors, each of which combine to produce a single off-rafting potential.

(5) $S_i^{off} = c_i \beta_{i,j} d_i^*$

In this way, the off-rafting equation consists of a set of coefficients multiplied with the number of currently rafting species, c_i. Each coefficient consists of a number between 0 and 1, depending on the ecological characteristics of the rafting community and the given ecoregion. Thus, the lower each coefficient parameter is, the lower the number of total species off-rafting in ecoregion i. The 'ecosimilarity' parameter β represents the similarity of one ecoregion to another. Specifically, β is a ratio that compares the ecological characteristics of the current ecoregion (i) with those of the native ecoregion (j) of each currently rafting species (while individual species data is not stored in the model, we retain information about the number of species that on-rafted in each ecoregion). In this way, the 'ecosimilarity' value represents the suitability of each rafting species to the conditions of the current ecoregion. Thus, the more different the current ecoregion is to the native ecoregion of a species, the lower the chances that species can successfully off-raft. The off-rafting equation also includes a parameter d_i^*, which represents the average depth (in ratio form) of each ecoregion. It's important to note here that in this model, we use two different average depth variables, d_i and d_i^*. Unlike the d_i parameter used in the on-rafting equation, d_i^* is a ratio that represents the depth of the current ecoregion relative to the mean ecoregion depth. In this way, the depth value of each ecoregion plays an important role in the establishment probability of rafting species, while retaining the same 0-1 coefficient format as the ecosimilarity matrix. Together, the off-rafting equation gives us a value for dispersed larvae per raft, per ecoregion, depending on the number of rafting species, and the biophysical limitations of that ecoregion.

i = Ecoregion where plastic raft is located at current time

x = Time spent in ecoregion i

β = 'ecosimilarity' of ecoregion i to native ecoregion of rafting species j

d = average ecoregion depth

c = species richness on raft at ecoregion i

c_{max} = maximum plausible on-rafting rate of species in ecoregion i at time t

P = source population of species in ecoregion i

S = number of alien species on- and off-rafting in ecoregion i

E = extinction rate of species on raft in i

n, R = species-specific variables

* = parameters where variable is converted to coefficient

A = average island area

D = island distance from mainland

D_0 = average species dispersal distance

S = number of existing species on island

Figure 7: *List of equation variables and their corresponding parameters. Variables in black are those used in our model equations, and those in light grey are additional variables used in Gilpin and Diamond's equations that we do not implement. All variables are described in detail in Section 2.2, and parameter calculations are described in section 2.3.*

2.3   Calculation of Model Parameters

2.3.1 Ecosimilarity Matrix ($\beta_{i,j}$)

The ecosimilarity parameter is visualized as a matrix of all possible combinations of ecosimilarity values. To produce a single matrix of values that compare the characteristics of each ecoregion to each other, we assume the most relevant ecological characteristics to be ocean temperature and ocean salinity. In ocean ecosystems, these factors are known to be the primary limiting factors for alien species viability (Droghini et al., 2020). While additional factors could potentially have been included in the 'similarity' calculation, such as net primary productivity or dissolved oxygen content, the multiplicative nature of the ecosimilarity calculation allows for the addition of these factors in future work. Rasterized ocean temperature and surface salinity datasets are broadly available and were gathered from the UK's Center for Environmental Data Analysis (CEDA) for the year 2020 (average), along with a shapefile of the 232 marine ecoregions via databasin.org. These datasets were uploaded into ArcGIS (v3.0), and the Calculate Zonal Statistics function was used to calculate both average temperature and average sea surface salinity for each of the 232 ecoregions (Figure 8). In Python (v3.11.3), Sorenson-Dice similarity coefficient (Dice, 1945) was used to calculate the similarity of all ecoregions to all others, for both temperature (deg C) and salinity. The two resulting matrices were multiplied together elementwise, producing a single matrix of ecosimilarity values. Each value in this matrix is between 0 and 1, with lower numbers representing less similar ecoregions. A few polar ecoregions with average temperatures below 0 degrees Celsius produced ecosimilarity values of 0 (relative to warmer ecoregions), but we assume this to be a realistic assumption due to the biophysical limitations of subzero water temperatures (Aronson et al., 2007). Ultimately, the 'ecosimilarity' parameter serves to determine the reproductive viability and survivability of off-rafting species in novel ecoregions, based on the biophysical characteristics of their native ecoregions (Wilson, 2022).
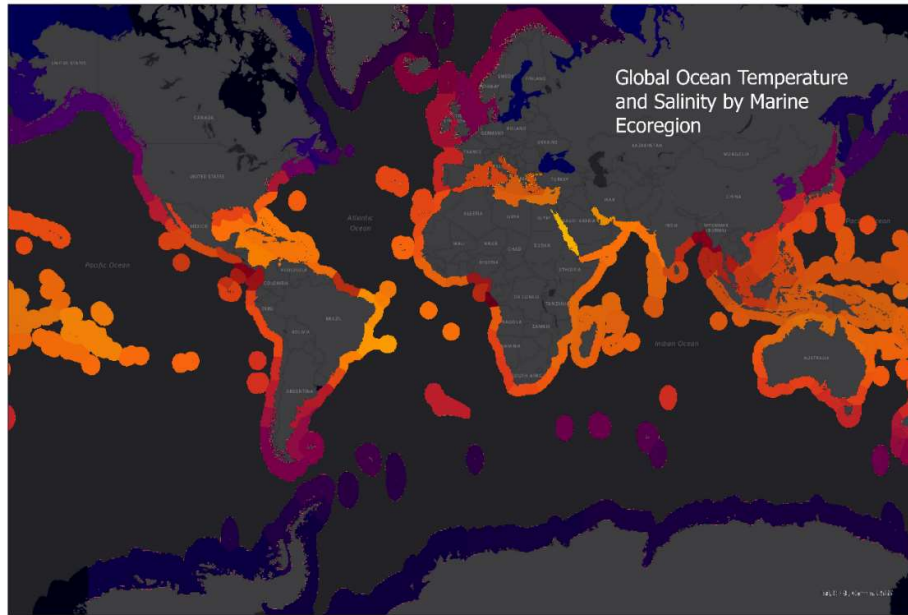
Figure 8: *Global ocean temperature x salinity by marine ecoregion. Average ocean temperature and salinity per ecoregion were calculated individually, then combined visually using multiplicative layering in ArcGIS (v3.0). Similar colors represent similar 'ecosimilarity' values for each ecoregion.*

2.3.2 Maximum On-Raft Rate ($c_{\max,i}$)

The c_{max} parameter is an equation that represents the change in species richness over time. The equation is based on a study of the 2011 Japanese tsunami debris data, which became a valuable case study in alien species propagation as the debris spread across the Pacific Ocean over the following decade. As one part of this, Carlton et al. (2017) recorded species abundance on a range of rafting objects over the course of 6 years (Figure 9a). Different categories of objects exhibited different species compositions, with the 'other' category including the most common forms of plastic debris. We took the data from this category and re-plotted it in Excel. With this, we created an exponential (degree 2) best fit curve, exhibiting an upper asymptote and a quadratic equation (Figure 9b). This equation, however, represents species richness over time; in order to include the equation in our on-rafting model, we needed a rate of change in species richness. Thus, with the derivative of this equation, we could calculate an average on-rafting rate for a specific time period. Using the dates recorded in the ocean parcels model for a debris object's travel time in each ecoregion, we calculate an average on-rafting rate for each ecoregion travelled through. However, since this data is acquired from only a single dataset, it is unclear whether this value represents a high, low, or average estimate of species richness. Here, we assume this dataset to be an average-case scenario, and we increase the resulting rate of change by 20% in order to represent an extreme scenario. It is important to note that the best-fit curve displayed in Figure (9b) exhibits zero on-rafting earlier than about t=400 days; to compensate for this lack of on-rafting in early time periods (which is quite

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unrealistic, given the ETIB), we have set a minimum on-rafting rate of 5 species per ecoregion. The remaining on-rafting equation parameters subsequently serve to reduce the on-rafting probability, depending on the ecoregion characteristics and plastic object's behavior. Thus, the c_{max} simply represents a realistic maximum on-rafting value based on the time component of the plastic object.
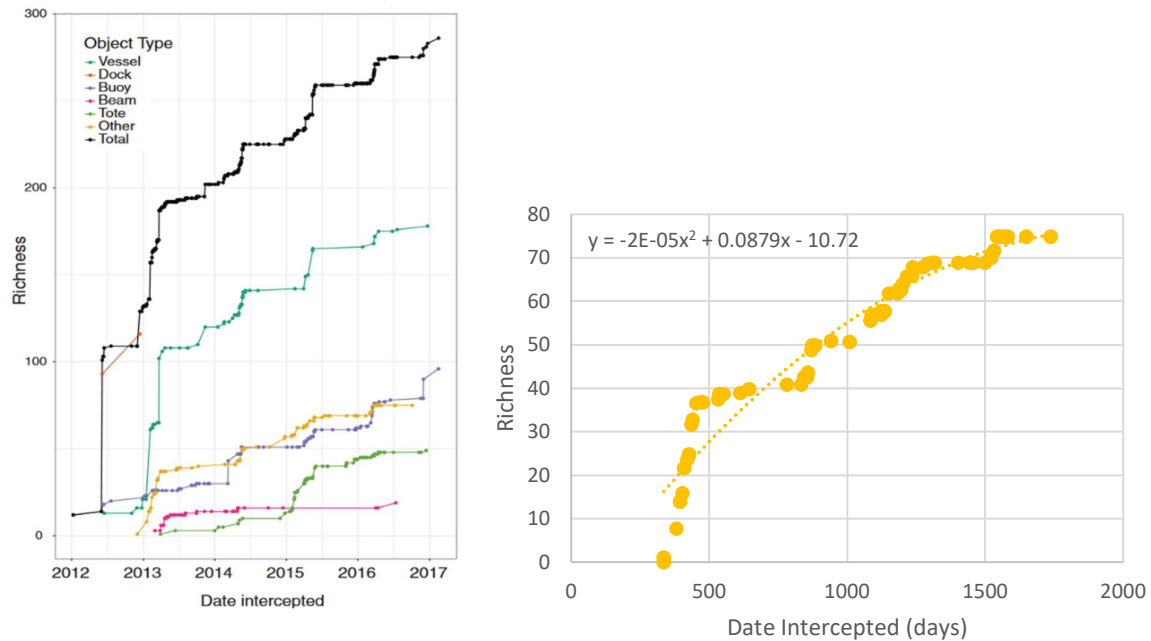
Figure 9a-b: *Species richness on a range of rafting types over a period of ~5 years from Carlton et al., 2017 (a). The data from the 'other' category was used to calculate c_{max} in this model. The 'other' data is displayed in better resolution in (b), alongside the quadratic best-fit equation (dotted line) which represents c_{max}. The derivative of c_{max} is used in the on-rafting equation, along with the time component, to calculate the maximum plausible value of on-rafting species per ecoregion.*

2.3.3 Average Depth by Ecoregion (d_i)

The average seafloor depth of each ecoregion (d_i) was calculated using publicly available bathymetry data and spatial analysis tools in ArcGIS. Bathymetry data was collected from the General Bathymetric Chart of the Oceans (GEBCO) as eight different raster tiles, representing the eight half-quadrants of the earth's surface area (i.e., one quarter of a hemisphere). These raster files were uploaded into ArcGIS (v3.0) and converted into a single raster dataset using the Mosaic to Raster tool. Similar to the ecosimilarity matrix, a shapefile of marine ecoregions was layered on top of the bathymetry data, then average depth by ecoregion was calculated using ArcGIS's Zonal Statistics tool. This analysis

provided an average seafloor depth for each marine ecoregion, which was converted into a csv file for use in the on-rafting equation.

Using this data, a proportional version of average depth by ecoregion (d_i^*) was created in excel, representing the average depth of each ecoregion relative to the mean of the average depths recorded. In this way, it was possible to convert true depth measurements into a coefficient ≤1, which could subsequently be implemented in the off-rafting equation in each ecoregion. Originally, this parameter was designed to function as a scale between 0 and 1, with the shallowest ecoregion representing 1, and the deepest ecoregion close to zero. However, in practice, this method obtained off-rafting values that were nearly zero for all of the ecoregions below about 300m of depth, with an exponential decrease in value (Figure 10a). While establishment in deeper ecoregions is certainly more unlikely than in shallower ecoregions, the interconnectedness of ocean ecosystems means that depth is not the determining factor in the establishment of alien species in novel ecosystems (Jaspers et al., 2018). Establishment is much more dependent on temperature and salinity (Droghini et al., 2020). However, to include the reduced probability of establishment in extremely deep ecosystems, we have preserved the proportional depth parameter, but instead of depth relative to the minimum ecoregion value, we use depth relative to the mean (2241.9 m). All values above the mean are set to 1, and coefficients below the mean decrease roughly linearly to a minimum of 0.44 in the deepest ecoregion (Cocos-Keeling/Christmas Island). These values are displayed in Figure (10b). In this way, the d_i^* parameter limits establishment probability of off-rafting species in deep ecoregions. In shallower ecoregions, however, establishment is limited only by temperature and salinity.
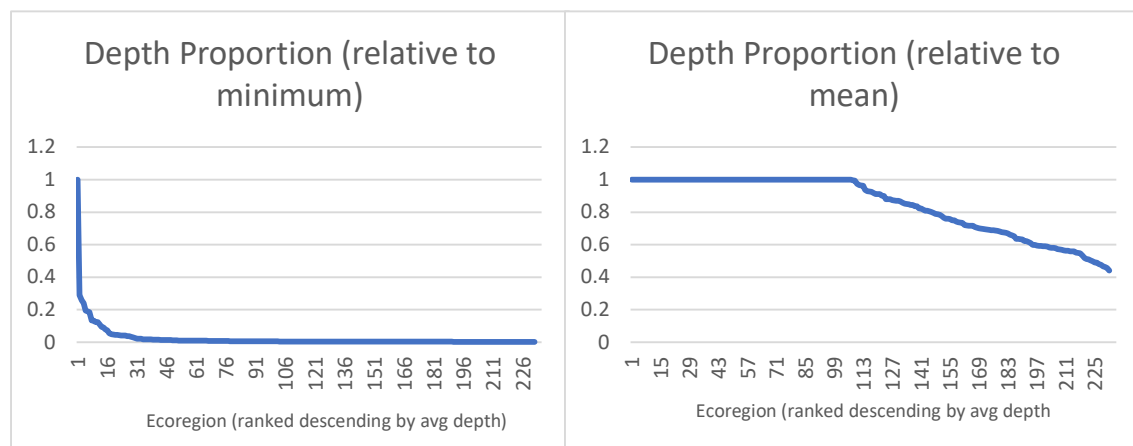
Figure 10a-b: *Proportional ecoregion depths relative to the minimum average ecoregion depth (a) and the mean average ecoregion depth (b). When depth relative to minimum is used, the depth coefficient value drops exponentially, drastically reducing the overall off-rafting equation values. However, when depth relative to mean is used, only extremely deep ecoregions limit the off-rafting potential of species, and even here, the off-rafting potential as a result of depth decreases almost linearly. Thus, we favor (b) for use in our model.*

2.3.4 Ecoregion Source Populations (P_i)

The source populations for each ecoregion represents the total number of resident species that can feasibly raft (see section 3.2.2). In terms of island biogeography, this represents the total number of species from a 'mainland' source population capable of immigration to any given 'island' For the purposes of this model, we use as a source population *all* species recorded in MarInvaders for each ecoregion (Lonka et al., 2021). All species have the potential to become alien, and this dataset represents the best estimate of source populations per ecoregion that exists. The specific species that on-raft in each ecoregion are not stored in the model, but a random 'batch' of species are selected from the total number of species in that ecoregion, based on the probabilities inherent in the remaining equation parameters. The number of species on-rafting in each ecoregion are then stored in the model, for use in the ecosimilarity parameter described in the off-rafting equation.

2.3.5 Distance Travelled per Ecoregion (x_i)

The parameter represented by x_i described the distance travelled in each ecoregion (i) by a single plastic object. This distance is calculated based on the OceanParcels fate model from Hoiberg et al. (in preparation). Coordinates for each plastic piece are recorded on a daily basis within the model run time frame. Distances are calculated as the length between each coordinate, then summed for each ecoregion the plastic object has travelled through. Since the time periods used for this model are quite long, the distances calculated here can be quite large as well. As a result, the effect of the linear approximation between coordinate-days on the overall distance calculation is negligible, and ultimately proves a reasonable portrayal of ocean plastic flow patterns.

2.3.6 Extinction Rate (r)

The extinction rate, r, used in this model is included in order to simulate the inherent probability of extinction for small populations of species in spatially limited habitats, such as rafts (MacArthur and Wilson, 1963). This extinction rate was calculated based on Gilpin and Diamond's extinction equation, using a raft species richness of 50 (about 2/3 of maximum), a raft area of $2m^2$ (based on the size of Japanese Tsunami debris in Carlton et al., 2017; reasonable given the high surface area of plastic netting and other objects), and an ecoregion travel period of 100 days (roughly average in our simulations). This calculation produced an extinction rate of 0.16, or 16% of species extinct per ecoregion. In the model, this value is subtracted from 1 and multiplied with the species richness per raft (at the beginning of ecoregion travel) to produce the number of species extinct during travel in that ecoregion.

2.3.7 Model Fit Parameter (n)

The model fit parameter, n, described in Gilpin and Diamond's 1976 work on Salomon Island birds describes a species-specific exponent, Diamond and Gilpin describe this parameter as being species-specific; in other words, its value will depend on how their model is applied, and will vary substantially across applications. In our equations, the exponential fit parameter plays an important role, by determining the relative importance of the rafting species – source population ratio (S_i/P_i, which plays an especially important role in the early stages of on-rafting, when existing species counts on the raft are low). Diamond and Gilpin use an exponential value of n=2.37 for the Salomon Island birds. However, they use this parameter for bird species, with much smaller mainland populations than as described in our model. Since we include all marine species recorded in MarInvaders, not just specific taxa, as our source populations, then the relative weight of the S_i/P_i ratio becomes incredibly small, to the point of negligibility (see sensitivity analysis in section 3.1.1). Thus, to compensate for the extremeness in this operation, we have selected a value of n=100 for this model (which provides a much more meaningful weight to the S_i/P_i ratio). This parameter isn't absolutely critical for calculating the rate of on-rafting species, but it serves very crucially to make the behavior of our model more biologically realistic and consistent with the ETIB.

2.4   Sensitivity Analysis

A sensitivity analysis was conducted for each of the parameters contained in the on-rafting equation (Equation 2a). In the off-rafting equation, a sensitivity analysis was irrelevant, as each of the parameters had equal weight in determining the result. The complexity of the on-rafting equation and the sheer number of parameters involved necessitated a sensitivity analysis. This was accomplished by calculating both absolute and relative sensitivity for each model parameter contained in the equation. Absolute sensitivity is calculated by taking the derivative of the given equation with respect to the parameter being tested. This derivative equation is quantified according to known parameter values, and the result is the absolute sensitivity. Relative sensitivity is the absolute sensitivity, multiplied with the ratio of the known parameter value being tested over the output of the original equation quantified with known parameter values. This was repeated for every parameter in the on-rafting equation. 'Known' parameter values were gathered from the South China run of our model, for a single ecoregion traversed by a single plastic particle ('Central Kuroshio Current', travelled by particle 0). These parameter values were measured as P_i = 5900 species, c_i = 10.05 species, d_i = 2894m, x_i = 2503157 m, n = 2.3 (later changed to 100 in the model), and $c_{\max i,t}$ = 1.4 species. The results of our sensitivity analysis are documented in section 3.1.1.

3 Results and Discussion

3.1 Model Results

3.1.1 Sensitivity Analysis

The results of our sensitivity analysis are included in Table (1). For each on-rafting parameter, we calculate both absolute and relative sensitivity. Absolute sensitivity tells us how much the equation output changes when we change a parameter value by 1. Relative sensitivity allows us to compare sensitivity across parameters. Together, these sensitivities allow us to see the relative importance of each parameter in the final model output. Not only does this allow us to better understand the functionality of our model, but it also allows us to look for sources of improvement for future iterations of these equations.

Table 1: *Results of sensitivity analysis for each parameter included in the on-rafting equation. Includes both absolute and relative sensitivity for each parameter. Negative values indicate negative changes to equation output from positive changes to the parameter.*

Parameter	Absolute Sensitivity	Relative Sensitivity
P_i	1.846 E-6	0.007849
c_i	-1.084 E-3	-0.007849
d_i	-9.106 E-7	-0.001899
x_i	6.408 E-10	0.001156
n	-4.731 E-3	-0.007842
$c_{\max i,t}$	0.9910	1

Each of the parameters measured (except $c_{\max i,t}$) exhibit extremely low absolute sensitivities. These values may be useful for understanding equation behavior, but they may be heavily dependent on the specific parameter values used for this calculation (i.e., extremely low values do not necessarily indicate useless parameters). For the purposes of understanding model limitations, relative sensitivity is more useful. Here, we see quite low values (on the scale of E-3) in all parameters except $c_{\max i,t}$, which maintains a value of 1 because it is a simple multiplicative coefficient in the equation. These low sensitivities are largely due to the fact that each of these parameters are contained in some form of an exponential functional; while exponentials have an important role to play in the

mathematical behavior of our equations, they also serve to heavily limit the relative impact of each parameter contained therein. One of the positive aspects of this equation is the fact that n, a correction variable, is itself the exponential. As a result, increasing n essentially allows us to increase the relative sensitivities of c_i and P_i. This is extremely useful for fine-tuning model performance. Because d_i and x_i are contained within a base e exponential, this is not possible in the current version of our model equation but from a biogeography standpoint, these are the least important parameters in the equation. As discussed in section 3.1.1., time is probably more important than distance travelled in determining species colonization, and a time component is already included in the $c_{\max,t}$ parameter. Further, depth can be used as a proxy for migration distance, but the interconnectedness of the ocean negates the importance of this parameter relative to traditional island ecosystems. Ultimately, this sensitivity analysis demonstrates the relative importance of the c_{max} parameter in determining the on-rafting rate (and thus, the relative importance of the time component contained within c_{max}). This analysis is critical for painting a complete picture of model functionality.

3.1.2 OceanParcels Model

The Ocean Parcels plastic distribution model was implemented using the parameters discussed in section 2.1.3. The results of this model are displayed in Figure (11). This geospatial portrayal of plastic routes demonstrates the wide range of possible plastic fates for a single release point in the South China Sea. These 50 particles interact with a total of 9 marine ecoregions. 6 of these plastic particles end up in the Pacific Gyre (indicated by particles travelling off the right side of the map), where they largely remain for the duration of the model runtime. This reflects the strong tendency of Pacific Ocean currents towards the gyre, which can be easily observed in the high number of plastic objects that become trapped here in the real world (Peng et al., 2021). Even these particles, though, travel through 3-4 different ecoregions before reaching the open ocean, allowing for plenty of species exchange along the way. Further, while many plastic particles end up in the pacific gyre, 16 of them wind up in other ecoregions. This range of fates include the coast of Vietnam, the northern coast of Japan, and South Korea. The variation captured here is likely due to both seasonal variations simulated in the model, as well as the stochastic sinking probability (which can be seen in the dataset as those particles whose trajectories end before the full model runtime). Finally, the majority of particles (28) remain in the South China Sea for the entire duration of the runtime. While these particles are useless for our own model, they are significant from a plastic management perspective: one country's waste management strategies will heavily affect its own ecosystems; not all plastic impacts are externalized. Still, the high prevalence of plastic particles remaining in the ecoregion of origin means 50 particles is probably too small a number to draw meaningful conclusions. In order to better estimate the effect of plastic releases on alien species proliferation, we will likely need to implement an OceanParcels model run on the scale of 100-1000 plastic particles in future model iterations.
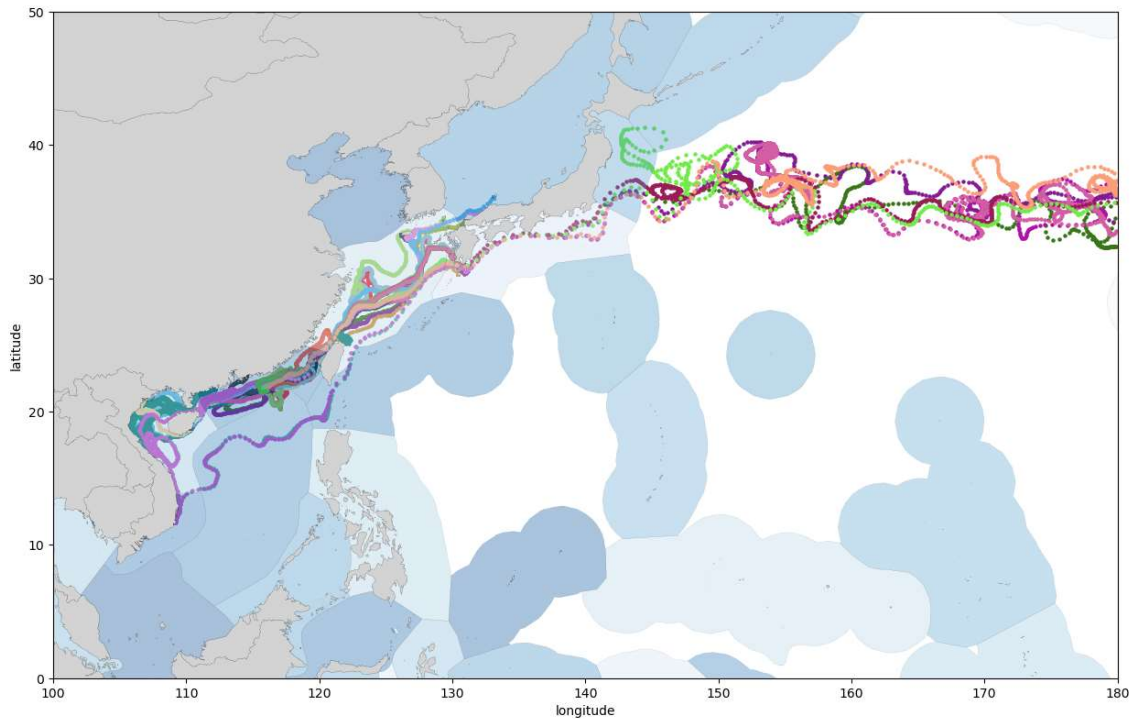
Figure 11: *Map of OceanParcels plastic flow model results. Each color represents a different piece of plastic as it flows through the ocean. Blue shapes represent marine ecoregions. All plastic objects drifting off the left side of the map end up in the pacific gyre. t = 8 years, n = 50 particles, release radius = 50km, release point = 'South China' ecoregion centroid.*

Broadly, the plastic trajectories captured in this model seem to accurately represent real world patterns of plastic drift. Existing ocean plastic models describe a strong tendency for ocean plastic to end up either on shorelines, the seafloor, or in ocean gyres (Chenillat et al., 2021) (Peng et al., 2021). This model reflects that same tendency, with the majority of particles ending in either the Pacific Gyre or remaining close to shore. While this model does not simulate beaching (i.e., particles washing on shore and remaining there), it captures the behavior of plastic particles before they meet this fate. Additionally, the tendency of plastic particles to remain close to shore supports the mechanism of the alien species model, which only functions within ecoregions. If plastic rafts remain largely within ecoregions (save those which end up in gyres), then our simulation of alien species flow appears to be a fair representation of this mechanism. Further, the range of plastic particle fates captured in this specific ocean parcels model simulation, as well as the wide range of ecoregions these particles intersect with, mean that these results are a reasonable framework on which to construct our invasive species model.

3.1.3 Alien Species Model (Single Iteration)

Using the 'South China' ecoregion as a release point, we first use a single hypothetical plastic particle trajectory to visualize our alien species model. This trajectory is shown in Figure (12). This trajectory represents a plastic particle which begins in the South China Sea, then travels north through 3 more ecoregions, before entering the deep ocean and spending the remainder of the model runtime trapped in the Pacific Gyre. As the figure shows, this route is relatively linear from source to sink, with only a few variations in particle speed throughout the journey (shown by the spacing of each observation point in Figure 12). Overall, this particle takes 229 days to travel from its release point to the open oceans. Considering a model runtime of 8 years, this means the particle spent the vast majority of its time in the open ocean, where the alien species model is not applicable. However, ocean travel is not necessarily a bad thing, it simply pauses the species flow occurring in the model. In fact, the alien species model is probably most relevant for plastic objects that exit and reenter ecoregions across the ocean, in distant regions of the world (where rafting species are more likely to be alien) (Goldstein et al., 2014). Further, the fact that this particle intersects with a total of four ecoregions, plus its relatively straightforward route and its long lifetime, make it useful for illustrating the efficacy of the model.
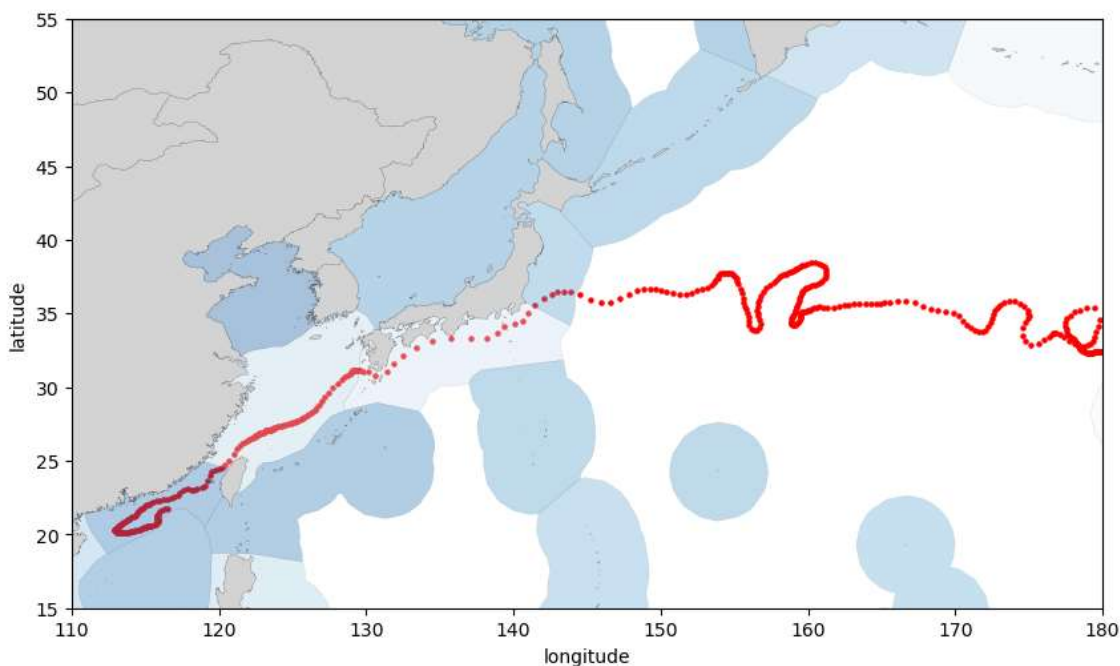

Figure 12: *Map of single plastic particle trajectory (in red) from OceanParcels model run. This object begins in the South China ecoregion, then flows through 3 additional ecoregions (colored in blue) before ending up in the Pacific Gyre (not shown). Used as test trajectory for alien species model.*

The species flows captured in this single trajectory are described in Figure (13). The ecoregions travelled through by this particle are, in order, 'Southern China', 'East China Sea', 'Central Kuroshio Current', and 'Northeastern Honshu'. The species richness on the raft at the end of travel in each ecoregion are, respectively, 4.9, 10.1, 14.8, and 13.4 (while it is physically impossible to have fractions of species on a piece of plastic, the species richness is stored as a decimal for future use in characterization factor development). Lastly, the number of off-rafting species per ecoregion travelled are, respectively, 0 (no off-rafting in start ecoregion, as all species on raft are already found here), 4.5, 9.4, and 9. These values generally follow the expected trend: increasing species richness on the raft through model simulation and corresponding off-rafting values. However, note the decrease in raft richness from the third to the fourth ecoregion (and corresponding decrease in off-rafting rates). This is likely due to our model's equation behavior: the travel time through the fourth ecoregion is quite short (Northeastern Honshu, 6 days). Thus, there is little room for on-rafting giving the short distance and time component here. Our model, though, maintains an extinction rate which is equal for every ecoregion encountered, regardless of the time component. The standardized extinction rate outweighs the smaller on-rafting rate, and thus raft richness decreases. In reality, it may seem unlikely that species richness can decrease with so little existing richness on the raft (e.g., due to a lack of competition or predation), but this mirrors the fluctuation that occurs around species equilibria in island biogeography. Losing 1-2 species is not at all unrealistic given the fluctuation in environmental conditions a rafting community experiences. Additionally, these off-rafting species numbers may seem relatively small, given the low chance of subsequent establishment in novel ecosystems (Pysek et al., 2020). However, it is important to remember that these numbers represent the impacts from a single piece of plastic, from a single release point in the oceans. Given the exorbitant volumes of plastic released into the oceans each year (Audrezet et al., 2021), these miniscule values can amount to substantial alien species impacts when aggregated on a global scale.
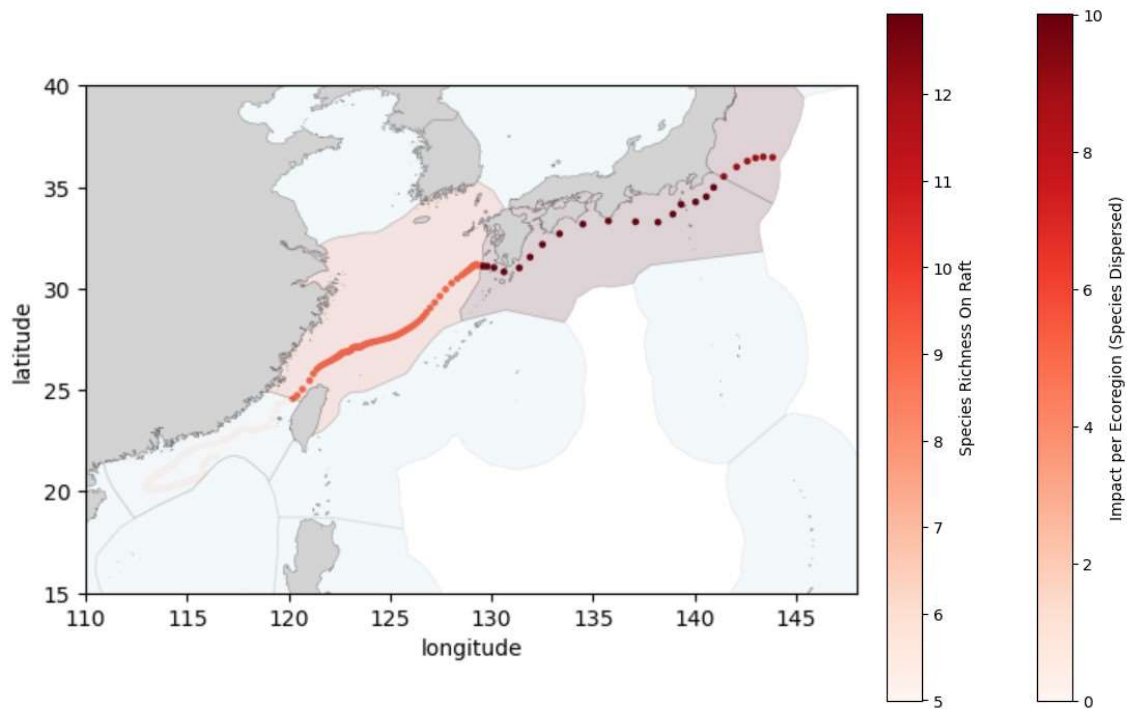
Figure 13: *Map of single plastic particle trajectory with species flows mapped on top. Changing colors of the plastic particle itself (dots) reflect changes in species richness on raft as it flows through different ecoregions (colored in light blue). Ecoregions the particle travels through are colored in various shades of red, depending on the number of species off-rafting per ecoregion. This value can broadly be seen as the alien species impact of the plastic raft per ecoregion.*

It is important here to discuss the biological implications of these results. It should be reiterated that this is a *model* and is not attempting to predict real-world flows of alien species in the past or the future. Rather, when aggregated on a large scale, this model should help identify areas of concern and quantify potential risk. Additionally, when this model describes a species as "off-rafting", what it really means is that species is reproducing, then its offspring enter the surrounding ecoregion. When these larvae enter a novel ecoregion, though, they are not automatically 'established' in that ecoregion. We do not necessarily assume that they survive, that they attach themselves to seafloor substrates, or that they cause any ecological damage to existing species. All this model attempts to describe is the introduction of theoretically larval species to a novel ecoregion as a result of plastic flows (the Effect Factor currently under development by Gjedde et al. will attempt to quantify the chances of establishment and subsequent ecological impacts resulting from the introduction of alien marine species). It is merely a way of understanding species flow patterns. In this sense, the trajectory described in Figures (12) and (13) is a useful means of visualizing the functionality of our model, but it is ultimately useless in terms of describing alien species risks. It represents a single 'sample size' with no statistical value. It is only when we aggregate across many plastic particles that we begin to get a clear picture of the alien species risks from this single plastic release point. Ultimately, our work was time-limited in terms of the scope of the model presented here. However, future work with our model will expand the scope of our analysis, first to encompass all 50 plastic

particles released from the Southern China ecoregion in this iteration of the OceanParcels model, then later, to encompass release points of a similar scale in all 232 marine ecoregions of the world.

3.2 Model Limitations

3.2.1 Plastic Fates

There are a few important components of rafting ecology that are not included in our model but require further discussion here. The ocean parcels plastic model does not differentiate between different forms or chemical compositions of plastic. However, plastic rafts can occur in a wide range of forms, from fishing gear to floating docks to drink bottles, and they do not all behave identically in the way they transport species (Carlton et al., 2017). A few studies suggest that the chemical and topological makeup of plastic debris plays an important role in determining which species attach themselves and for how long, but the extent to which this is true is still a matter of discussion (Garcia-Gomes et al., 2021). Nonetheless, the wide variation in shapes, sizes, and chemical composition of plastic debris means there are likely differences in the way rafting communities assemble themselves therein (Rech et al., 2016). There are also a wide range of other ocean debris types that we do not model here. Natural debris, such as driftwood, often has short lifetimes relative to plastic debris, and exists in relatively small quantities in the ocean (Barnes and Milner, 2005). Numerous other types of anthropogenic debris have also been found in the ocean, each with unique chemical compositions, and as a result, species compositions (Ibabe et al., 2020) However, due to the overwhelming prevalence of plastic in ocean debris, as well as generalizations built into the ocean parcels model, we do not include variations in raft substrates in our model.

While plastic rafts tend to exhibit extremely long lifetimes, there are a range of possible fates that can occur over the lifetime of a raft. Our model covers a two-dimensional map of the ocean surface, but rafting is inherently a three-dimensional process. Plastic has been found in all parts of the water column, from ocean surfaces to the bottom of the Mariana Trench (Audrezet et al., 2020). In many documented cases, floating rafts become saturated with species to the point that they become denser than the surrounding water, thus sinking down into the water column (Thiel and Gutow, 2005). Especially in the case of smaller plastic objects, this phenomenon prevents many alien species from reaching distant ecosystems, where the highest invasion impacts could occur (Goldstein et al., 2014). The plastic model developed by Høiberg et al. (in preparation) includes a sinking probability for individual pieces of plastic, which is thus incorporated into our model as well. However, this probability is not based on raft saturation or other biotic parameters that may affect raft density. Future model improvements could include some stochasticity in the fate of plastic rafts, with increasing disappearance probabilities as a raft becomes increasingly saturated with species. If raft size were to be included in such a model as well, probabilities could vary with raft size such that smaller objects are much more subject to sinking effects than larger ones.

In addition, the range of plastic particle fates captured in this model does not include beaching. While much is still unknown about the true fates of ocean plastic, it is increasingly clear that a large portion of ocean plastic ends up on the world's beaches (Peng et al.,

2021) (Chenillat et al., 2021). The ocean parcels model, however, assumes all plastic either sinks or remains in the open ocean. As a result, this model probably overestimates the lifetimes of ocean plastic in surface ecosystems. Consequently, our model probably overestimates the spread potential of species rafting on this plastic. If more plastic objects became beached, there would be fewer vectors for alien species proliferation. If a beaching rate were built into the ocean parcels model (provided there was sufficient data to estimate it), it could be easily incorporated into the alien species model as well. This is another means of future model improvement, as beaching is an important aspect of ocean plastic dynamics.

3.2.2 Species Composition

One important limitation of our model is the simple fact that not all marine species are capable of rafting. This 'capability' is captured in our model as ecoregion source populations (the parameter P_0). in the current development phase of the MarInvaders database, it is impossible to sort species in each ecoregion by taxonomy (though this will be possible in future versions). As a result, all species in MarInvaders were marked as 'rafting capable'. Given the importance of taxonomy in rafting ecology, it is prescient to discuss here potential ways to include this parameter in future models. Our initial literature review reviewed existing field studies in order to compile a semi-comprehensive list of all possible rafting taxa. The vast majority of observations (81%) consisted of species in a narrow range of taxa: primarily *Mollusca, Arthropoda, Cnidaria* and *Bryozoa*: all largely sessile marine species (Carlton et al., 2017) (Garcia-Gomez et al., 2021) (Goldstein et al., 2014) (Rech et al., 2018). This may also indicate a strong sampling bias in these measurements towards larger marine fauna. Regardless, the taxa excluded from most rafting samples were both pelagic taxa (whose entire life cycles are lived suspended in the open ocean, e.g., *Ctenophora*), as well as vertebrate species. In theory, pelagic and vertebrate species are capable of 'rafting', in the sense that they can follow a raft as it travels through the ocean and derive their nutrients from its resident species. However, they are never physically bound to the raft, so they are not entirely dependent on it for transport and survival. Additionally, the chances are unlikely that these taxa would embark on the same long-distance journeys as sessile rafting species, if their doing so is not necessary for survival (Thiel and Gutow, 2005).

Thus, taxon (on the level of order), as well as mobility, are likely useful predictors for a species' rafting capability. Still, challenges persist in predicting 'raftability' for a single species. Until now, species composition has primarily been studied through field analyses of rafting objects found in the ocean (Astudillo et al., 2009) (Miller et al., 2016). Such studies are useful for understanding common patterns in raft colonization and ecology, but they are not comprehensive. In other words, it's impossible to say that a species categorically *doesn't* raft if it simply hasn't yet been found on a raft. Furthermore, the taxa that exhibit a preference for natural rafts often do not exhibit the same preference for plastic rafts (Pinochet et al., 2020). Further field studies of species preferences for raft types would serve to provide more specific classifications for rafting species. Such data would allow us to, for example, assign weighted probabilities to taxa who show higher preferences for rafting over others (i.e., some species may exist in higher proportions on rafts than in their native ecoregions, such as mollusks). This would reduce some of the

model's randomness in selecting on-rafting species from each ecoregion, constructing model raft communities that more closely resemble reality.

In the real world, the species composition of rafts can vary substantially over time as well (Ibabe et al., 2020). As has been observed in many branches of succession ecology, the species that initially colonize a piece of debris are generally well-adapted to a wide range of environments, reproduce rapidly, but decline in abundance when subject to competitive pressure from other species (Thiel and Gutow, 2005). Conversely, many late-successional species struggle to colonize new debris, but once established, can create durable populations. In this way, the rafting community can change substantially over time, and these successional changes have been demonstrated in a number of field studies (Tsikhon-Lukanina, 2001). While some forms of natural debris may enter ocean environments with a range of species already established (e.g., mangrove root systems), plastic is generally quite 'clean' in the early phases of rafting. Thus, it most likely follows a traditional pattern of ecological succession, depending on the substrate (Goldstein et al., 2013). This model does not include temporal variations in species composition as a result of succession. Model improvements in this area could include lower establishment probabilities (S^{on}) and higher survival probabilities ($1-r$) for late successional species included in the MarInvaders Database, for example (Wilson, 2022).

3.2.3 Resolution and Scale

The ecoregion scale used in this model has a few important functionalities: it a) allows us to model global flows of species, which as mentioned previously, may be more ecologically significant than localized spread; b) ignores the more complex, local dynamics of species spread and plastic flow, which is more stochastic and heavily dependent on short-term ocean currents; and c) allows us to incorporate the MarInvaders database into our model. However, one important consequence of using ecoregions as the functional scale of the model is the limited coverage they provide. Together, the ecoregions described by Spalding et al. (2007) do not cover the entire ocean surface; they cover all the world's near-shore ecosystems, but they leave out the deep ocean. In terms of model functionality, this means that we record zero on- or off-rafting behavior in deep oceans, and species composition remains constant across all trans-oceanic voyages. In the case of invasive species, however, this model choice can be ecologically justified: first, deep ocean regions are less biodiverse than coastal ecosystems, so the impacts of alien species would be smaller or nonexistent (Spalding et al., 2007); second, it is highly unlikely that deep-ocean benthic species that can travel all the way to the ocean surface, then subsequently attach themselves to floating rafts; and third, in the opposite direction, it would be extremely difficult for any 'unrafting' species' larvae to attach themselves to seafloor substrates in deep oceans. While it is possible that these larvae may drift in ocean currents and establish themselves in near-shore regions elsewhere, this mechanism is extremely stochastic and the invasive species impacts are negligible. There are still likely local extinctions that occur in the rafting community as the plastic object drifts through deep ocean, but these considerations have been excluded from the model.

The global resolution of this model also excludes small-scale spread of invasive species within ecoregions. This has some important implications for our model's functionality: as mentioned previously, we forego some of the stochasticity inherent in small-scale dispersal

patterns of marine species; we also assume the specific range limits of each individual species to be the geographical boundaries of the ecoregions they have been observed in. However, this ignores some of the ecological realities of rafting. First, we aggregate the impacts of IAS to whole ecoregion; however, invasive species may have greater impacts in some parts of an ecoregion than another (due to differences in biodiversity or community structure). Similarly, a species may not be alien to one part of an ecoregion but may be entirely novel in another. These small-scale biogeographical variations are inherently excluded from an ecoregion-scale analysis. Second, another common vector through which anthropogenic debris amplifies the spread of IAS is through 'secondary spread' (Audrezet et al., 2021). In this process, invasive species are introduced to areas of high human activity (e.g., a port, via shipping activity), and from there, floating anthropogenic debris serves to distribute these species further into surrounding marine ecosystems. Numerous field studies have demonstrated the prevalence of secondary spread in busy port regions (Miralles et al., 2018) (Ibabe et al., 2020), and as shipping is historically the world's primary vector for marine IAS transport, secondary spread may play a critical role in amplifying the resulting biodiversity impacts (Molnar et al., 2008). Studies of *Macrocystis pyrifera* in the Southern California Bight suggest that natural rafts seem to play an important role in maintaining marine ecosystem connectivity on a local scale, which may help to distribute existing alien species via secondary spread as well (Hobday, 1999). The ecoregion scale used in this model means we ignore the role of secondary spread in marine IAS impacts. However, future analyses can combine the existing plastic model with global shipping models to identify potential secondary spread hotspots (Wilson, 2022).

3.2.4 MarInvaders Database

MarInvaders is a user-friendly database designed to document and describe the prevalence of alien marine species in ecoregions worldwide (Atlantis-ERC, 2021). It is based on existing sightings of marine species in each marine ecoregion, both native and alien. Thus, MarInvaders is an extremely powerful tool for centralizing and visualizing all existing marine invasive species data. However, it is important to note that it is limited in the fact that it relies on observations for its data. As with any observational data, it is subject to the human biases inherent in field sampling (Liu et al., 2022). The MarInvaders data likely skews towards larger, more visible animal species, which means the plethora of algae and plant species previously found on rafts may not be reflected in this dataset (Carlton et al., 2017). Our model does not currently incorporate taxa filters, but these biases may prove a challenge in future iterations. MarInvaders also makes the same assumptions about species ranges and impacts as our model (see section 3.2.3), since it describes species ranges using marine ecoregions. Finally, MarInvaders records species sightings, but does not document the extent or abundance of each species within an ecoregion. As a consequence, our model gives each resident species an equal chance of on-rafting. In most cases, though, there is huge variation in the abundance of individuals within each ecoregion, and therefore huge variations in their access to potential rafts (Wilson, 2022).

3.2.5 Equation Behavior

Depending on the specific routes of each plastic object, the model equations have some important functional limitations. First, as the sensitivity analysis demonstrated, the parameters vary substantially in terms of their relative sensitivities. Specifically, in the on-rafting equation, we see huge weight given to the maximum on-rafting per ecoregion parameter. This variable is critical for setting the values of the on-rafting equation to a reasonable range. However, this parameter is based only on the 8-year Japanese Tsunami debris data, and would serve as a more reliable metric if there were a wider range of field data to draw on. Furthermore, this parameter is largely what determines the on-rafting values per ecoregion and is only slightly modified by the remaining equation parameters. In this sense, this equation is somewhat ecoregion-specific, but the broader model would be well served by an on-rafting equation that was more situationally sensitive. The exponential parameter, n, plays a role in this process by amplifying the relative values of existing raft and source population richness, and this parameter can be modified according to the model requirements. The second exponential term (base e, which includes distance travelled and ecoregion depth), however, cannot be modified to become more less sensitive, and thus plays only a minor role in the model. Increasing the relative sensitivity of this operation should be a focus of future model improvement (e.g., use a different base value or exponential).

The off-rafting equation has proved to be a robust method for quantifying alien species dispersal, but its limitations lie in its simplicity. Unlike the extinction equation, though, the off-rafting equation can be easily modified to more accurately calculate species dispersal, simply by adding additional coefficients. For example, the ecosimilarity parameter can be refined to include net primary production or dissolved oxygen content, beyond the existing temperature and salinity. One important coefficient to include here would be one based on the raft's distance travelled per ecoregion. The dispersal rate of species on the raft is very likely related to the amount of time they spend in that ecoregion; however, our model does not take the distance travelled into account for off-rafting at all (due to challenges in calculating this parameter in a similar format). This could include a coefficient calculated in a similar way to the average ecoregion depth coefficient, with longer travel routes maintaining a value closer to 1 and shorter routes closer to 0, based on some reference distance.

Finally, the off-rafting equation has the interesting effect of increasing off-rafting rates in ecoregions closer to the ecoregion off origin. In other words, nearby ecoregions, with high ecosimilarity values, lead to higher off-rafting rates than more distant ones. In many ways, this is balanced by the time-dependent species richness on each raft, but it highlights an important limitation of our model: how large really are the impacts of alien species in adjacent ecoregions? Since we don't track taxa or species characteristics, it's impossible to know whether the off-rafting species are truly alien in the adjacent ecoregions, or if they already exist there and their ranges simply extend into both ecoregions. Thus, this model may be substantially overestimating the alien species impacts of rafting in ecoregions close to the ecoregion of origin. It may be useful to include in future models a coefficient that represents the similarity of biological communities in each ecoregion, based on MarInvaders data, for example. Alternatively, the model could begin tracking specific species by randomly selecting species from ecoregion source populations for on-rafting, then cross-checking that species with known species ranges in subsequent ecoregions. If this off-rafting species already existed in that ecoregion, then alien species impacts would

be 0 for that species. These are just examples, but such solutions would allow us to reduce the apparent impact of alien species in ecoregions that are adjacent and similar in species composition (i.e., where alien species are unlikely to actually be alien). Overall, the model equations presented in this paper serve as a strong foundation for the rafting model. Each individual parameter is grounded in some form of field data or known rafting ecology, and they have contributed to reasonable model outputs thus far. Moving forward, however, the limitations described here are all important avenues for model improvements.

3.2.6 Gilpin and Diamond's Model and Translatability of the ETIB

Section 2.1.2 describes the translatability of the Equilibrium Theory of Island Biogeography to applications in plastic rafting. The ETIB has proven to be a robust theory with many applications in ecological modelling, including the model presented here. However, there are some limitations to its application to plastic rafting.

We have relied heavily on Gilpin and Diamond's (1976) application of the ETIB to provide a mathematical underpinning to our model. It is important to note that Gilpin and Diamond's work is focused solely on immigration/extinction rates, with functions based on species richness that are fitted to the quintessential curves of the ETIB. While these equations are all based on biologically meaningful parameters, the rates themselves are meaningless except to describe equilibrium species richness. These 'rates' are basically ratios with no units (e.g., not quantified as species/day). However, the integration of our model in LCIA necessitates quantifying these rates to create species richness values. As part of this, we have modified the original equations to produce a model output in units of species. In other words, we have taken a unitless, parameter-dependent rate and multiplied it by a time-dependent species count to produce an on-rafting value (as discussed, this was deemed mathematically pointless with the extinction rate, so we used a simple extinction rate). It is worth pointing out that this is somewhat of a departure from Gilpin and Diamond's original purposes for these equations; but it is simply a difference of data availability. Gilpin and Diamond worked backwards from robust, long-term field data, creating equations which drew together their field data and the ETIB. Their equations exist to mathematically predict equilibrium species richness, provided certain parameters are already quantified. We, however, know from the JTMD data what equilibrium species richness should roughly look like in the rafting community. Therefore, we aim to construct model equations that reach these equilibrium values across a range of scenarios, without relying too heavily on individual datasets. We do this by quantifying a wide range of ecoregion-dependent parameters and combining them in a way that sticks closely to the original ETIB theory. Thus, in a broad sense, the ETIB relies on stable extinction-immigration rates that, with small variations, may drastically affect the equilibrium species richness. We, on the other hand, rely on a fairly stable equilibrium species richness, which can be reached through a number of different parameter-dependent extinction-immigration scenarios. This fundamental distinction does not, we think, affect the validity of our model as a whole; rather it simply reflects the challenges we have faced in constructing a biologically meaningful model based on the ETIB.

Another critical difference between our model and ETIB theory is in the model fit parameter n. Gilpin and Diamond implement n as a parameter which serves to give the immigration and extinction curves their distinctive concave shapes (see Figure 5). While 'shape' may

seem somewhat arbitrary, a linear immigration-extinction curve essentially assumes zero competition between species. These interspecific interactions are a critical component of island biogeography and ecological models as a whole. Since, according to Gilpin and Diamond, this parameter is model-specific, we were required to make a model choice here. Gilpin and Diamond used a value of 2.3 to best fit their field data. We have no field data, so the choice was somewhat arbitrary, and challenging in terms of accurately tweaking the output of our model. As discussed in section 2.3.7, we chose a value of 100. We believe this value provides the model with increased ecoregion specificity and biologically realistic behavior, without affecting the results beyond the point of reasonability. Again, this model choice is somewhat arbitrary, but we look to further studies in rafting ecology to provide us with more robust data to improve our model fit.

Further, our extinction equation neglects the exponential parameter n entirely. Here, a model choice was necessary: either we could calculate a daily extinction rate based on the number of existing raft species using Diamond and Gilpin's equation (using the constants they used to describe Salomon Island bird populations), then multiply this by the days spent in each ecoregion in order to get the number of species extinct per ecoregion; or, we could use a more simplified extinction rate, with a single coefficient representing the death rate per ecoregion (i.e., independent of raft travel or existing species richness). The former scenario, though more dynamic, leads to extreme extinction rates when the rafts spend long periods of time in a single ecoregion, and the number of species is near equilibrium (roughly half of all species locally extinct after 400 days). While this may be a realistic extinction rate in island ecosystems, the apparent resilience of rafting communities makes this rate seem extreme in our model (Barnes and Fraser, 2003) (Haram et al., 2023). Furthermore, our integration of this model with the alien species effect factor means that units are important; each equation had to be in units of species. Thus, it made the most sense for the extinction equation to be a simple linear expression. Further model improvements should, critically, include more accurate extinction estimates, and if possible, exponential extinction rates to better model the inter-specific dynamics of island biogeography on each raft. Like many aspects of this model, these limitations are largely due to a lack of more comprehensive field data on rafting ecology.

Gilpin and Diamond's equations are based on data from bird communities in the Salomon Islands. In many ways, birds are the ideal model organism for island biogeography studies. They are conspicuous species, with easily predicted dispersal distances and fairly consistent migration patterns. This supports Gilpin and Diamond's work in the sense that it demonstrates the robustness of their underlying dataset. The use of birds as model organisms, however, means their population models may be less transferrable to more complex communities of organisms. Their fundamental models rely heavily on their own field data. As such, some of the 13 equation sets they test that fit well with their own data might not apply in other contexts. We build our model off the most accurate of their thirteen equation sets with the assumption that it is broadly applicable (as Gilpin and Diamond attest), but it may be the case that this equation set does not function well in the context of raft communities. The only way to reduce this inherent uncertainty in our model is with a more robust set of field data to draw from.

3.3 Outlook and Future Research

Future work with this model may include a number of additional steps:

- Expand our model scope to encompass all 50 (or more) plastic particles described in the OceanParcels data implemented in our model.

- Fully globalizing the model for incorporation into the characterization factor - run the model for all 232 ecoregions, then aggregating the results into country-specific impacts.

- Improve off-rafting estimates with a more detailed ecosimilarity matrix (include net primary production, etc.), as well as a 'community similarity' parameter, which minimizes 'accidental' alien introductions.

- Modifying the extinction equation with more ecoregion-specific parameters (i.e., beyond just a linear extinction rate).

- Filter ecoregion source populations by taxa to create a more realistic raft community assemblage (not necessary for incorporation into a characterization, but useful for increasing model specificity).

- Additional raft disappearance probabilities based on the saturation of species on each raft, or on known beaching rates.

Future work will largely consist of implementing this model as an exposure factor within the impact dimension of life cycle assessment. Initially, this will look like a matrix of values, ecoregion by ecoregion, representing the number of species introduced to each ecoregion as a result of plastic released in each other ecoregion. On a practical scale, this can be calculated by taking the impacts on each ecoregion by every plastic particle modelled in a single simulation. Then, by summing these impacts and dividing by the total number of plastic particles simulated, we get an average impact on every ecoregion as a result of plastic released from a single ecoregion. By doing this for every ecoregion, we can compile the matrix discussed above. Then, by aggregating or dividing ecoregions into national boundaries, this matrix can be converted into a country-by-country matrix. Combining this matrix with the fate and effect models will thus produce estimates for biodiversity impacts from alien species as a result of plastic released from a single industrial process. This may require further model refinement and parameter quantification, but our work here lays a strong foundation for future applications in LCA.

Within the broader field of invasion ecology, there are a number of interesting avenues of research this model may provide. Within the scope of the model itself, improving its grounding in ecological reality will help support or modify the assumptions we have made in constructing it. For example, modifying the ecosimilarity matrix to incorporate a wider range of ecological parameters would provide a more detailed understanding of species' establishment probabilities in novel ecosystems. More importantly, though, more comprehensive, long-term field studies of rafting communities will go a long way towards improving our model robustness. For example, more complex analyses of rafting ecology (including successional changes, habitat complexity development, reproduction rates, and growth/extinction rates) would allow us to more accurately model the development of

rafting communities over time. Additional long-term studies of existing rafting communities on plastic objects (such as the JTMD study) that record resident species and ecoregions of origin would provide us with real-world on-rafting rates which we could use to validate our results. This model could also be supplemented with a more dynamic description of invasion probabilities of plastic flows over time. Currently, the model makes broad averages for plastic's flow across ecoregions; but integrating the changing position of plastic debris within ecoregions over time, as well as variations in depth and ecosimilarity, would more accurately describe the flow of invasive species within ecoregions. Finally, as discussed previously, existing models and datasets could be used to model secondary spread of invasive species on a more granular scale, as a result of both shipping processes and plastic flows. These two models in tandem would provide a more detailed description of the true impacts of marine invasive species on global biodiversity (Wilson, 2022).

Our work represents a genuinely novel combination of industrial ecology methods and biogeographical theory. We hope this work creates fertile ground for future research in both of these fields. Invasion ecology is a challenging subject of study, with limited data availability, little public attention, and exceedingly complex policy outcomes. While managing the impacts of invasive species is difficult, it is nonetheless important to recognize the role they play in global biodiversity loss. A critical piece of this puzzle is understanding how, and where, our own activities help or hinder the problem. As such, industrial ecology and LCA have an important role to play in the field of invasion ecology moving forward.

Some sections of Results and Discussion based on that of my own master's project. Cited as (Wilson, 2022) where relevant.

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Data Sources:

https://databasin.org/datasets/3b6b12e7bcca419990c9081c0af254a2/

https://data.ceda.ac.uk/neodc/esacci/sst/data

https://data.ceda.ac.uk/neodc/esacci/sea_surface_salinity/data

https://www.gebco.net/data_and_products/gridded_bathymetry_data/

marinvaders.atlantis-erc.eu/

Appendices

Appendix 1: SI1 – Rafting species sightings database (from our own literature review). Attached as a .xlsx file.

Appendix 2: SI2 – Ecosimilarity matrix. Attached as a .xlsx file

Appendix 3: SI3 - Average salinity by ecoregion, calculated using ArcGis. Attached as a .xlsx file.

Appendix 4: SI4 - Average temperature by ecoregion, calculated using ArcGis. Attached as a .xlsx file.

Appendix 5: SI5 – ArcGis project file used to calculate ecosimilarity matrix.

Appendix 6: SI6 - Japanese tsunami richness data used to calculate maximum richness.

Appendix 7: SI7 – Python file for code used to calculate both the maximum richness value and the ecosimilarity matrix. Attached as a .py file.
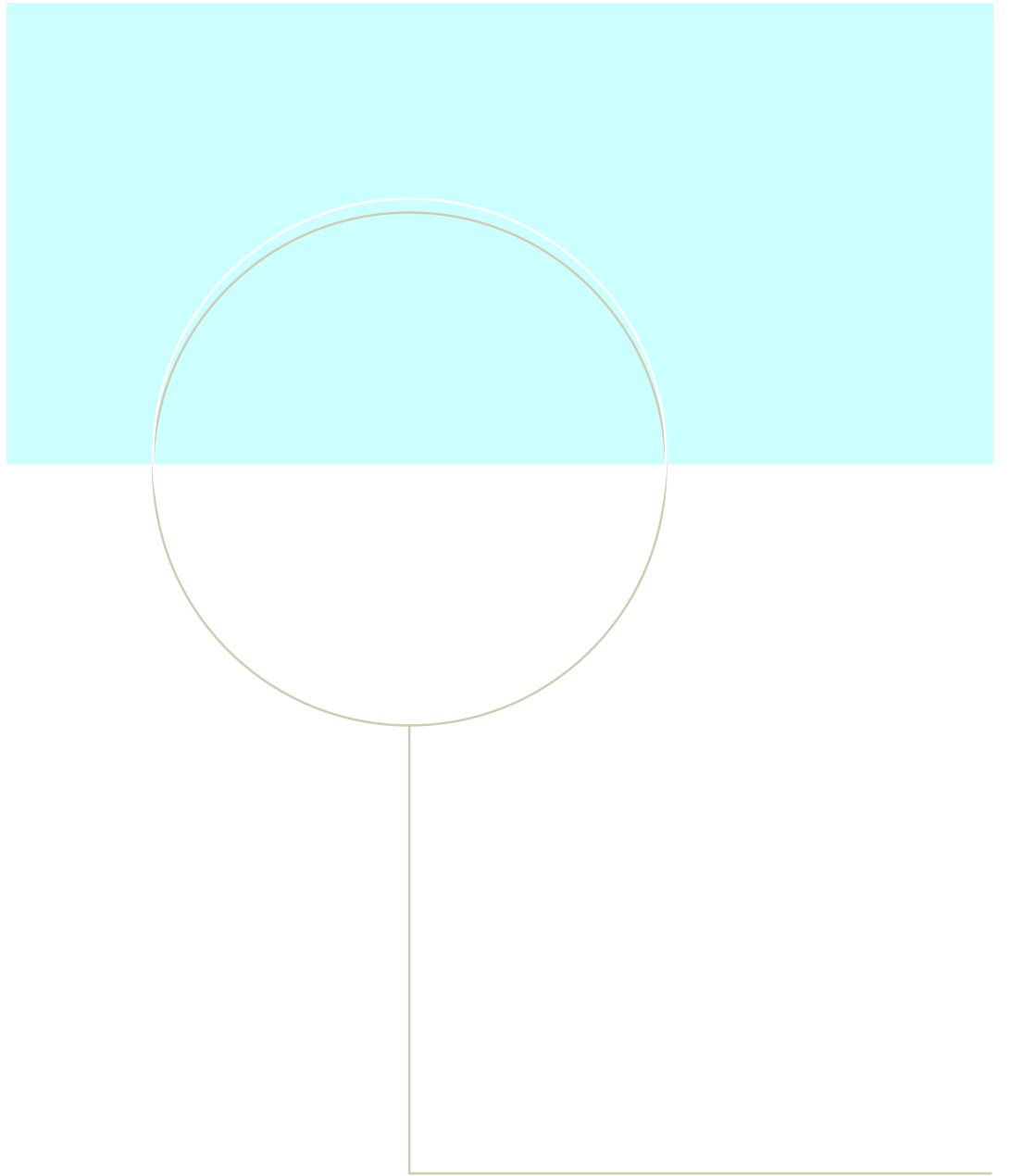
Appendix 8: SI8 – ArcGIS project file used to calculate average depth by ecoregion.

Appendix 9: SI9 – Average depth by ecoregion. Attached as a .xlsx file.

Appendix 10: SI10 – Data on species richness by marine ecoregion from MarInvaders. Attached as a .xlsx file.

Appendix 11: SI11 **-** Data from OceanParcels model run in South China. Attached as a .csv file.

Appendix 12: SI12 – Python file for code used in main model calculations. Attached as a .py file.