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Volcanic Impacts on Coral Reefs

Jan-Christopher Fischer

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the degree of Master of Science by Research in the Faculty of Science.

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Bristol, United Kingdom

November 2022

Word count: 25,644

Abstract

Considering the current coral reef crisis and given the conservation priority of tropical reefs, better understanding of the drivers shaping ecological coral reef resilience is required to direct contemporary management strategies. Despite the relevance of volcanic impacts in shaping coral development throughout evolution, they have received little scientific attention. Here, selected case studies are presented to identify and describe unifying patterns of volcanic implications on coral reef communities. An important volcanic hazard affecting coral reefs is material deposition from tephra fallout, pyroclastic currents, and lava flows. Volcanic activities can directly impact coral reefs by material deposition during eruptive periods, and subsequently alter habitat conditions from local to global scales. Related changes affect water quality and substrate characteristics. Coral reefs cannot form on loose volcanic substrates, whereas stable volcanic bedrock provides important shallow-water habitats to corals and other reef organisms. Volcanically-induced habitat changes may persist for months to millennia depending on hazard intensities, ecological reef state, species composition, and environmental conditions. However, coral communities are able to recover from volcanic impacts and in some instances, can even enhance local reef biodiversity and stimulate species turnover. In this study, critical hazard thresholds of coral reef responses to volcanic impacts from tephra deposition are defined. Integrating those references into probabilistic tephra fall modelling in the Coral Triangle (CT) allowed for hazard quantification in space and time. The CT is a global hotspot of marine biodiversity alongside active volcanism hosts some of the most diverse coral reef communities. In this region, over 42% of coral reefs are likely to be affected by light volcanic impacts within 1,000 years. However, the probabilities for most severe events with tephra deposition of 30 cm and the potential to eliminate entire coral reef communities are low only with 6% of coral reefs potentially affected within a millennia.

Acknowledgments

I thank my supervisors, Dr Erica Hendy, Dr Elena Couce, and Dr Susanna Jenkins, for their scientific input, feedback, and guidance. I am especially grateful to my supervisors for giving me the chance of being part of the H2020 Marie Skłodowska-Curie Innovative Training Network 4D-REEF. I have learnt a lot and it was inspiring being part of this Innovative Training Network.

Special thanks goes to Prof Dan Lunt for his support.

I would like to thank Prof Willem Renema, Chantal Huibers, Caroline van Impelen, and Chantal Cornelissen for the organisation of project activities during network training activities in the Netherlands and in Spain. Also, thanks to all my friends and colleagues, the early stage researchers from the 4D-REEF project.

Joshua Measure-Hughes has helped a lot with the implementation of the Tephra2 model – thank you, Josh!

I am happy that I have met Xin Ren, Brian Chen, Qian Liu, Anne Eberle, Madleen Grohgan, James Kershaw, Khalil Imran Abdul Rahman, and all other colleagues making my time at the University of Bristol enjoyable. Furthermore, Lauren McEnnis, Tom Russell, Oliver Board, Benjamin Perfect, and Helena Denton made a big difference to my life in Bristol – thanks!

Last, but not least, I am most thankful to my partner, Anna Walentowitz, my parents, Gudrun and Rainer Fischer, and my siblings, Katharina, Benjamin, and Theresa, for their trust and support in some difficult times in the past.

It has been good exploring Britain's great nature and countryside with many wildlife observations of urban foxes in Bristol, badgers, muntjacs, and deer in Leigh Woods as well as porpoises in the Severn Estuary. I am thankful for those encounters.

Funding

This work is a part of the H2020 Marie Skłodowska-Curie Innovative Training Network 4D-REEF funded by the European Commission.

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the *University's Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Jan-Christopher Fischer

Bonn, 23rd November 2022

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1. Chapter 1 – Introduction

1.1. Volcanic impacts on coral reefs – an overview

Coral reefs are highly complex ecosystems shaped by calcifying organisms, most visibly scleractinian corals (Bellwood et al. 2004; Knowlton et al. 2010). By providing structurally rich benthic habitats, coral reefs support a large proportion of marine organisms (Bellwood et al. 2005) and effectively shape coastal geomorphologies (Darwin 1842; Spencer and Viles 2002). Consequently, human populations rely on coral reefs for a multitude of ecosystem services of significant economic value (Kittinger et al. 2012; Moberg and Folke 1999; Woodhead et al. 2019). As a consequence of human use, coral reefs around the globe are affected by multiple anthropogenic stressors including destructive fishing, coastal development, marine pollution, physical destruction, and global warming (Burke et al. 2012; Hughes et al. 2017). Impacts from human activities add to the natural disturbance regime characterizing coral reefs. Natural perturbations, such as storm impacts, extreme weather events, climatic variations, disease, and predator outbreaks, but also tectonic activities like earthquakes and volcanism (Goldberg and Wilkinson 2004; Wilkinson 1999), constantly affect coral reefs (Hughes and Connell 1999) and thus have shaped coral reef ecosystems over evolutionary times (Buddemeier and Smith 1999; Stanley, Shepherd, and Robinson 2018). At reef scale, volcanic activities can completely destroy all benthic life by burial, sedimentation, breakage, or removal (Eldredge and Kropp 1985; Reuter and Piller 2011; Vroom and Zgliczynski 2011) whilst additionally changing water and substrate conditions (Maniwavie et al. 2001; Tomascik, van Woosik, and Mah 1996). However, reef formation is not necessarily terminated by volcanic disturbances but coral proliferation and carbonate production can be limited (Dana 1872; Pandolfi et al. 2006; Reuter and Piller 2011). The impacts originating from volcanic activities as natural disturbances to coral reef ecosystems are subject of this thesis.

Scientific knowledge on volcanic impacts on coral reefs is limited. Infrequency and unpredictability of eruptions (Pyle and Barclay 2020) in combination with dangerous surrounding conditions (Smallhorn-West et al. 2020; Vroom and Zgliczynski 2011), have constrained empirical observations and therefore limited studies of volcanic effects on marine biota (Bearden et al. 2005; Heikoop, Tsujita, Heikoop, et al. 1996; Smallhorn-West et al. 2020). Rapid burial by pyroclastic material has benefitted science by preserving snapshots of complete coral reef communities through geological history (Montaggioni and Martin-Garin 2020; Pandolfi et al. 2006) but less is known about more

frequent and moderate volcano-coral reef-interactions (Reuter and Piller 2011; Schils 2012; Vroom and Zgliczynski 2011; Wu et al. 2018). Similarly, studies on ecological recovery of coral reef ecosystems, individual species or specimens following volcanic disturbances are rare, and typically focus on large-magnitude events with striking effects on reef benthic communities (Eldredge and Kropp 1985; Heikoop, Tsujita, Risk, et al. 1996; Maniwavie et al. 2001; Pajaro et al. 1992; Smallhorn-West et al. 2020; Tomascik et al. 1996; Vroom and Zgliczynski 2011), or exclusively address certain species (Barber, Moosa, and Palumbi 2002; Starger et al. 2010) and taxonomic groups (Hess et al. 2001; Ochavillo, Hernandez, and Aliño 1992; Putra 2020).

While a limited number of scientific records of volcanic impacts on coral reefs exist (Barber et al. 2002; Eldredge and Kropp 1985; Reuter and Piller 2011), there is an spatial bias among the available publications with a regional focus in southeast Asia. This region includes the Coral Triangle (CT) which is not only the contemporary global hotspot of marine biodiversity (Fidelman et al. 2012; Hoeksema 2007; Renema et al. 2008; Roberts et al. 2002) but also forms the westernmost edge of the Pacific ‘Ring of Fire’ with ~20% of the world’s active volcanoes (Global Volcanism Program 2022) (Fig. 1.1). Hosting more than 700 species of reef-building corals (Hughes, Connolly, and Keith 2013), this Indo-Pacific region is home to over 75% of global coral diversity (Veron et al. 2009). Almost half of the coral reefs in the region are located within 500 km of an active volcano and many lie in the vicinity of multiple vents (Fig. 1.2).

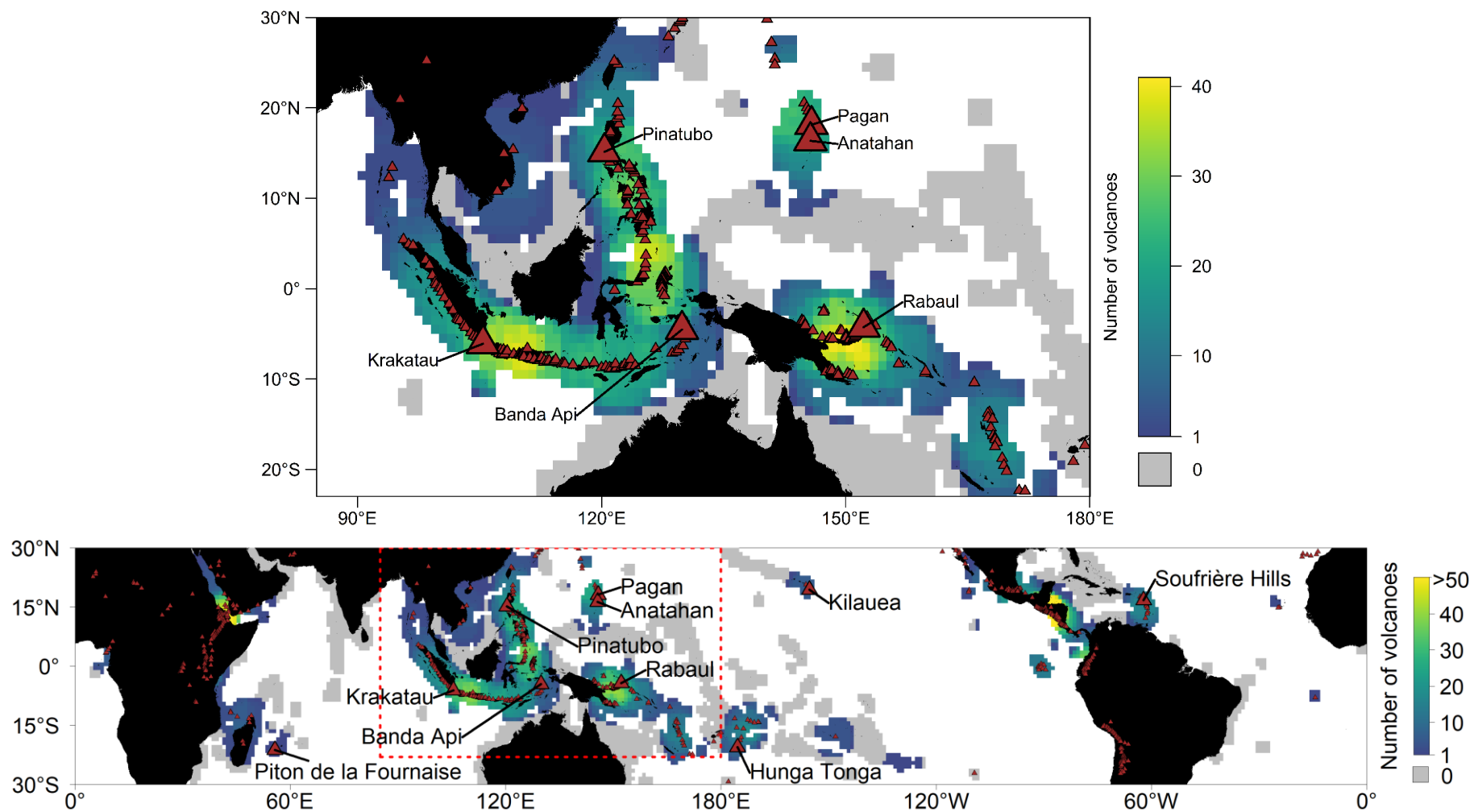


Figure 1.1: Numbers of active volcanoes within 500 km of global tropical coral reefs (bottom) and in the CT (top). Volcanoes are displayed by small red triangles. Case studies detailed in the following sections of this study are marked by larger labelled triangles. Volcano locations were extracted from the Global Volcanism Program database (Global Volcanism Program 2022). Spatial data on coral reef distribution was provided by the United Nations Environment Programme’s World Conservation Monitoring Centre, the WorldFish Center, the World Resources Institute, The Nature Conservancy (UNEP-WCMC et al. 2010). Reef areas were aggregated to 1° spatial resolution. The extent of the wider CT region (85-180°E, 30°N-23°S) shown in the top part is outlined by the dotted red rectangle in the global map. Terrestrial surfaces were obtained from Natural Earth (<https://www.naturalearthdata.com/>).

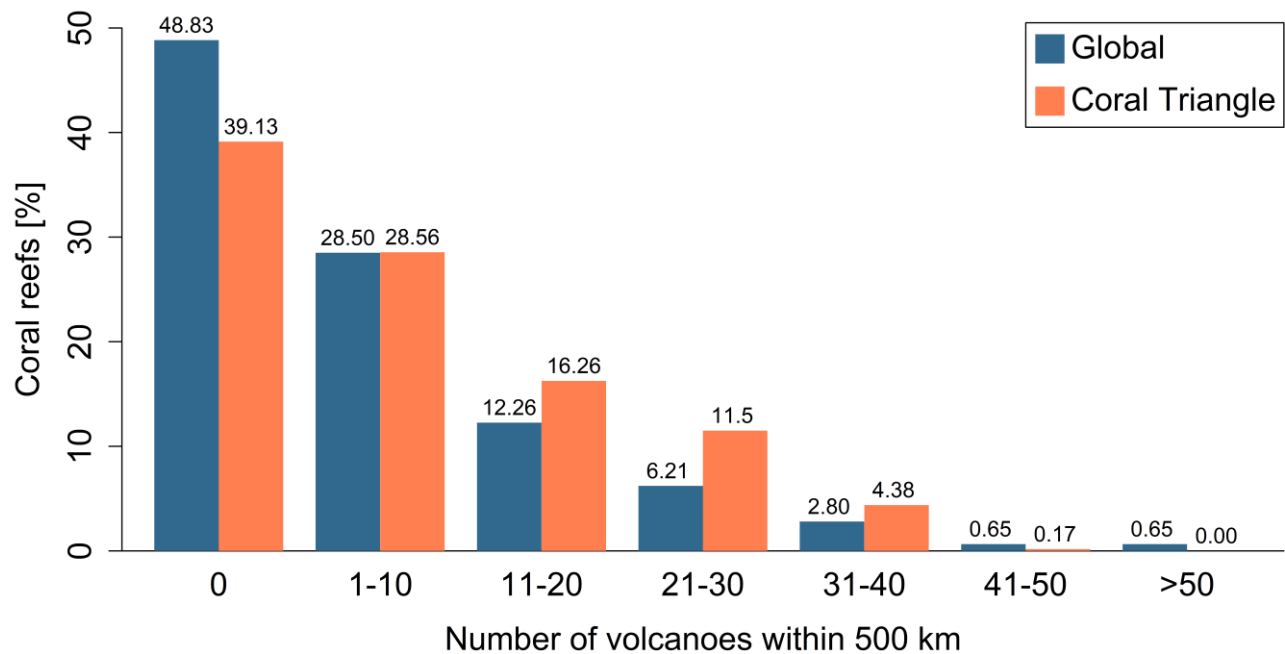


Figure 1.2: Percentages of tropical shallow water coral reefs with increasing numbers of volcanoes in spatial proximity of 500 km at global scale and in the Coral Triangle (CT).

In the current disturbance regime in the Anthropocene, volcanism is still a key environmental control factor to coral reef development (Huang et al. 2018; Wilson and Lokier 2002; Zhan et al. 2006) and distribution (Mutaqin 2020). Considering the current coral reef crisis (Bellwood et al. 2004) and given the conservation priority of tropical shallow-water reefs (Bellwood et al. 2019; Roberts et al. 2002), better understanding of the drivers shaping ecological coral reef resilience is required to direct contemporary management strategies and inform stakeholders at risk (Bellwood et al. 2004).

1.2. Rationale and outline

To date, volcanic hazard assessments have primarily focused on human population (Jenkins, McAnaney, et al. 2012; Magill and Blong 2005) and health (Carlsen et al. 2012; Hansell 2006; Horwell and Baxter 2006; Horwell, Baxter, and Kamanyire 2015), infrastructure at risk (Blong 2003; Jenkins et al. 2015; Mani, Tzachor, and Cole 2021; Wilson et al. 2014), and agriculture (Blong 1984b; Wilson et al. 2007). While primarily focussing on the most direct impacts volcanic activities have on humans, only minor attention was given to potential effects volcanic eruptions have on the natural resources people rely on.

This work aims to address this research gap by reviewing scientific records of volcanic impacts on coral reefs. A distinction between direct and indirect impacts aids bridging between the abiotic

(volcanic) triggers to biotic coral reef responses. Furthermore, scientific information on successional trajectories of coral reef ecosystems to recover from volcanic disturbances are compiled. Applied tephra fall modelling also allows for spatial and temporal hazard assessment with a particular regional focus set in southeast Asia.

2. Chapter 2 – Case studies

2.1. Selection of case study sites

To identify the variety of documented volcanic hazards and eruption effects on coral reefs, a focus was set on particular volcanic settings with the most extensive records of volcanic implications on coral reefs and organisms. All available reports including direct impacts associated with eruptions and indirect impacts from volcanically-induced environmental changes affecting coral reefs were considered. Respective literature was searched for via typical scientific web-based search engines such as Google Scholar and Web of Science.

The selected case studies originate from all tropical coral reef provinces. The ensemble comprises Krakatau (Indonesia), Pinatubo (Philippines), Banda Api (Indonesia), and Rabaul Caldera (Papua New Guinea) in southeast Asia, Piton de la Fournaise (Reunion Island) in the Indian Ocean, Mount Pagan, Anatahan (Northern Mariana Islands), and Kīlauea (Hawaii) in the North Pacific, Hunga Tonga–Hunga Ha’apai Island (Tonga) in the South Pacific, and Soufrière Hills (Montserrat) in the Atlantic Ocean. The locations of all volcanoes of the selected case studies are marked in the maps in Fig. 1.1. Geographical and volcanological information, predominant hazard types and reported impacts on coral reef organisms are detailed in Tab. 2.1.

Table 2.1: Volcanism case studies and summary of reported hazards to coral reefs. Volcano background information and eruption details were obtained from the Global Volcanism Program by the Smithsonian Institution (2022).

Volcano	Krakatau	Pinatubo	Northern Mariana Islands		Banda Api	Rabaul	Piton de la Fournaise	Kilauea	Soufrière Hills	Hunga Tonga–Hunga Ha’apai
			Mount Pagan	Anatahan						
Country, volcano type, tectonics	Indonesia, caldera, subduction zone	Philippines, stratovolcano, subduction zone	United States, stratovolcano, subduction zone		Indonesia, caldera, subduction zone	Papua New Guinea, pyroclastic shield, subduction zone	France, shield, intraplate	United States, shield, intraplate	United Kingdom, stratovolcano, subduction zone	Tonga, caldera, partially submarine, subduction zone
Earliest, last known eruption dates	250 ± 50 years, 2020	7460 BCE ± 150 years, 1993	1340 ± 100 years, 2021	2003, 2008	1586, 1998	683 ± 2 years	2800 BCE ± 150 years, 2022	~4650 BCE, 2022	8050 BCE ± 2000 years, 2013	1912, 2022
No. confirmed (uncertain) eruptions	55 (1)	8 (0)	20 (3)	4 (0)	23 (4)	19 (0)	191 (6)	96 (0)	9 (0)	5 (0)
Mode (min, max) VEI	2 (1, 6)	6 (1, 6)	2 (1, 4)	2 (2, 3)	2 (1, 3)	2 (1, 6)	2 (0, 5)	0 (0, 4)	3 (3, 3)	2 (0, 5)
Direct hazards to coral reefs	Pyroclastic influx, cone collapse, tsunami, sedimentation	Pyroclastic influx, tephra deposition, sedimentation	Tephra deposition, floating pumice, sedimentation, degassing	Tephra deposition, sedimentation	Lava flow, tephra deposition, sedimentation, hydrothermal venting	Tephra deposition, floating pumice, sedimentation, tectonic uplift	Lava flow, sedimentation, abrasion	Lava flow	Pyroclastic influx, sedimentation, dome collapse	Hydro-magmatic eruption, tephra deposition, pyroclastic influx, sedimentation
Indirect hazards to coral reefs	Substrate instability, water turbidity	Water turbidity, eutrophication, oxygen depletion, climatic implications	Water turbidity, substrate instability, water fertilization, overgrowth by sponge	Water turbidity, substrate instability	Water heating, substrate instability, acidification	Substrate instability, water turbidity	Substrate instability, light blocking	Water heating	Chemical water changes	Water turbidity, substrate instability, water heating
Selected references	Barber et al. 2002; van den Bergh et al. 2003; Carey et al. 1996, 2001; Mandeville, Carey, and Sigurdsson 1996; Putra, Damar, and Samosir 2014; Putra and Yulianto 2017; Sluiter 1890; Starger et al. 2010; Umbgrove 1930	Atrigenio, Aliño, and Biña 1991; Gagan and Chivas 1995; Genin, Lazar, and Brenner 1995; Gill et al. 2006; Hess et al. 2001; Kuhnert et al. 2000; Ochavillo et al. 1992; Pajaro et al. 1992; Wiesner, Wang, and Zheng 1995; Wu et al. 2018	Bearden et al. 2005; Eldredge 1982; Eldredge and Kropp 1985; Houk and Starmer 2010; Schils 2012	Bearden et al. 2005; Houk and Starmer 2010; Tribollet and Vroom 2007; Vroom and Zgliczynski 2011	Heikoop, Tsujita, Risk, et al. 1996; Januar et al. 2017; Sutarna 1990; Tomascik et al. 1997, 1996	Maniwavie et al. 2001; Munday 2000	Bollard et al. 2012; Jouval et al. 2020; Michon and Saint-Ange 2008; Montaggioni and Martin-Garin 2020; Pinault et al. 2013, 2014; Schleyer et al. 2016	Dana 1872; Gosline et al. 1954; Grigg and Maragos 1974; Moore et al. 1973	Myers 2013; Spalding, Ravilious, and Green 2001; Trofimovs, Sparks, and Talling 2008	Smallhorn-West et al. 2020

2.2. Krakatau

The Krakatau volcanic complex forms an archipelago in the Sunda Strait, Indonesia (Carey et al. 1996, 2001; Self 1992). There is limited information on Krakatau's activities prior to the cataclysmic VEI 6 event in 1883. In 1883, multiple Vulcanian and sub-Plinian eruptions caused tephra emission, and pyroclastic flow associated with caldera collapse and tsunami generation; the island was largely destroyed (Global Volcanism Program 2022; Self 1992; Self and Rampino 1981). The tsunami was generated by voluminous pyroclastic influx into the ocean at high discharge rates (Carey et al. 2001; Maeno and Imamura 2011; Self 1992). Waves up to 36 m high reached up to 10 km inland with heavy impacts along the exposed adjacent coastlines of Sumatra and Java (Carey et al. 2001). The total volume of erupted mass was estimated over 20 km³ (Self and Rampino 1981). Hot pyroclastic surges travelled more than 80 km over the sea and significant distant tephra accumulation was detected (Carey et al. 1996; Paris et al. 2014). However, most material was deposited within 15 km around the vent with subaerial pyroclastic flows vigorously mixing with sea water to result in the deposition of a basal material flow and turbidity current formation (Mandeville et al. 1996).

More than four decades after the 1883 eruption, a new cone formed within the caldera. Anak Krakatau first reached sea level in 1927 and has frequently been active ever since (Global Volcanism Program 2022). The young volcanic island constantly grew and attained an elevation of over 450 m in 2010 (Gardner et al. 2013; Simkin and Fiske 1983; Starger et al. 2010). In 2018, rapid material deposition into the coastal zone triggered a tsunami (Walter et al. 2019). Extreme geomorphologic dynamics characterize the volcanic complex due to ongoing eruptive activities, material deposition, and relocation (Carey et al. 1996, 2001; Mandeville et al. 1996; Self and Rampino 1981). Currently, three small islands form the mostly submerged caldera around Anak Krakatau (Global Volcanism Program 2022).

Narrow fringing reefs were reported from the volcanic complex prior to the eruption in 1883 (Sluiter 1890), but cone breakdown, shift of the coastline, and hot (475–550 °C) submarine pyroclastic flows produced during the 1883 eruption resulted in massive material deposition into the surrounding coastal waters (Mandeville et al. 1994; Sigurdsson et al. 1991). It is likely that all benthic biota was removed from the archipelago by this eruption (Barber et al. 2002; Simkin and Fiske 1983; Starger et al. 2010). Furthermore, distant tephra deposition, e.g., 50 cm ground tephra accumulation in South Sumatra 40 km from the vent (Carey et al. 1996), pyroclastic surges, and tsunami impacts, affected the surrounding islands and distant

coastlines (Carey et al. 1996; Mandeville et al. 1996; Starger et al. 2010). Physical destruction of benthic organisms by burial, breakage, and dislocation were reported from the shorelines in the Sunda Strait as a consequence of tsunamis in combination with other hazards from the eruption in 1883 (Carey et al. 2001; Putra and Yulianto 2017). Coral fragments interbedded in tsunami deposits were found in multiple locations up to ~80 km from the volcano (van den Bergh et al. 2003; Carey et al. 1996, 2001; Mandeville et al. 1996; Paris et al. 2014).

On the archipelago itself, initial coral recolonization on volcanoclastic deposits was found after five years (Sluiter 1890). However, harsh habitat conditions characterized by extreme erosion, continuous sedimentation, material reworking, and lack of stable substrates subsequently limited reef development (Sluiter 1890; Umbgrove 1930). As a consequence, the first recognized coral settlements could not be identified 50 years after 1883, but new formations of early coastal reefs were found (Umbgrove 1930). Frequent larval influx from distant resource refugia was found to have occurred post 1883 for scleractinian corals (*Pocillopora damicornis* and *Seriatopora hystrix*) and reef invertebrates (e.g., mantis shrimp) based on the elevated genetic diversity around Krakatau, relative to control sites in the Indo-Pacific (Barber et al. 2002; Starger et al. 2010). Pumice produced by the eruption, was suspected to be an exploratory factor of large marine species dispersal ranges (Jokiel and Cox 2003; Starger et al. 2010).

However, considering the younger volcanic past of the volcanic complex over the last decades, coral communities at Anak Krakatau were characterized by incipient stages of ecological succession. Typical pioneers, such as branching *Pocillopora* sp. and *Seriatopora* sp., were dominant. These first settling species found at Anak Krakatau in highest abundances were replaced by more specialized species at the surrounding outcrops without close-by volcanic impacts. Those changes were attributed to interspecies competition resulting in local coral assemblages dominated by massive *Porites* sp., furthermore including genera such as *Montipora*, *Acropora*, and *Millepora* (Putra et al. 2014).

Despite locally observed adverse habitat conditions with high water turbidity and unconsolidated substratum (Barber et al. 2002), a recent assessment of Krakatau's reef health concluded "fair to good" conditions of the benthic communities with cover estimates of 25-53%, 0-24%, and 14-40% for hard, soft, and dead corals respectively (Putra 2020). However, this assessment was undertaken before Anak Krakatau's partial cone collapse in 2018 (Walter

et al. 2019) which most likely impacted the local coral reefs (Putra 2020). No more up to date reef assessment from the Krakatau volcanic complex exists.

2.3. Pinatubo

Mount Pinatubo is a stratovolcano located in Central Luzon, Philippines. The history of Pinatubo's documented activities comprises a few, mostly high-magnitude eruptions (VEI 5-6). The cataclysmic event in 1991 (VEI 6) was one of the largest volcanic eruptions in the last century causing environmental and climatic effects around the globe (Global Volcanism Program 2022). This activity and the resultant environmental effects were for the first time monitored by Earth observation satellites making Pinatubo's eruption in 1991 a common reference for comparison with more recent volcanic activities (Jäger et al. 1995). The tephra plume emitted during the Plinian event reached into the stratosphere (Self et al. 1993) and resulted in tephra fallout in Luzon and over the South China Sea (Wiesner et al. 2004, 1995). Dome growth and extrusion associated with extreme tephra emission and pyroclastic flows transformed the former summit lava dome into a 2.5 km wide caldera (Global Volcanism Program 2022; Rosi et al. 2001). Subsequent pyroclastic deposition, downstream sedimentation, and lahars caused ongoing hazards up to tens of kilometres from vent (van Westen and Daag 2005; Wolfe and Hoblitt 1996). Lahar effects were seasonally triggered by monsoonal rain and occurred for years after the eruption (Janda et al. 1996; Rodolfo et al. 1996). The emission of around 17-20 million tons of sulphur dioxide affected the global atmospheric radiation balance with direct implications in terms of surface temperature cooling (Hansen et al. 1992; McCormick, Thomason, and Trepte 1995; Self et al. 1993; Stenchikov et al. 1998).

Local impacts on coral reefs are reported from the coastline of Zambales around 30-50 km from the vent where tephra fallout reduced shallow-water live coral cover from ~50% to below 10% (Pajaro et al. 1992). Similarly, volcanic material transport into the coastal zone resulted in a decline of post-eruptive fish biomass by 23-69% associated with hard coral cover reductions within three months after the eruption. The observed ecological impact abated with distance from the volcano reflecting a deposition gradient (Ochavillo et al. 1992). Coral cover losses were primarily attributed to smothering by tephra, water turbidity, and ongoing sedimentation (Atrigenio et al. 1991; Ochavillo et al. 1992).

Looking at more distal but direct impacts, deposition from tephra fallout following the 1991 eruption affected vast regions of the South China Sea (Wiesner et al. 2004, 1995). Volcanic sediments drastically altered habitat conditions with lethal consequences for benthic biota (Alve 1999; Hess et al. 2001; Lokier, Wilson, and Burton 2009). For example, tephra layer thickness was a critical factor for the diversity of foraminifera assemblages which were significantly different at sites with high tephra thickness closer to vent (> 3 cm) compared to more distal locations with lower tephra accumulation (< 2 cm) (Hess et al. 2001). At Son Tra Island in central Vietnam massive *Porites* colonies exposed to tephra influx stopped growth and died after 5-6 months, but were recolonized 2-3 months later (Wu et al. 2018). Here, tephra particles were found embedded in regrown coral tissue and persistent elevated rare earth element (REE) concentrations in the *Porites* skeletons indicate impacts over months from reworking of volcanic materials by terrestrial runoff and wave energy at coastal sites along the Vietnamese coastline (Wu et al. 2018). Corals in open ocean locations showed minor impacts. Here, adverse impact from tephra influx were mitigated by dilution and water circulation (Wu et al. 2018).

The large Pinatubo eruption in 1991 furthermore caused indirect impacts on coral reefs around the globe. Emitted stratospheric aerosols caused abrupt global cooling of -0.5°C (Hansen et al. 1992; McCormick et al. 1995; Self et al. 1993; Stenchikov et al. 1998) with variable impacts for coral reefs. For example, rates of coral bleaching in the Caribbean were reduced by a factor of five due to reduced El Niño strength (Gill et al. 2006). In contrast, in the Gulf of Aqaba in the northern Red Sea, extensive coral die-off and overgrowth by filamentous green algae (*Enteromorpha* sp.) occurred as a consequence of a weak thermal stratification within the water column (Genin et al. 1995). The upwelled nutrient-rich deep water stimulated a phytoplankton bloom with measured chlorophyll concentrations over four times higher than normal. Stony coral were covered by dense algae mats reducing water circulation, oxygen and light availability. For example, mortality of mushroom corals (*Fungia granulosa*, *Fungia horrida*, and *Ctenactis echinata*) locally exceeded 70% (Genin et al. 1995), whereas more resistant massive corals such as *Porites* sp. increased heterotrophy (according to changes in carbon isotopic signals in skeletal material deposited through the event; Felis et al. 1998) and mortality was under 10% (Genin et al. 1995).

2.4. Northern Mariana Islands

The Northern Mariana Archipelago in the western subtropical North Pacific consists of nine emergent islands of which six were volcanically active in the past century (Houk and Starmer 2010; Trusdell et al. 2005). Located west of the Mariana Trench, the archipelago rises from the Pacific and Philippine subduction zone (Bearden et al. 2005). While eruptive activities vary between the volcanoes of the island chain, effects on coastal coral reefs are manifold (Houk and Starmer 2010). Steep relief in combination with unconsolidated volcanic material and strong wave exposure, causes unfavourable environmental conditions for coral settlement (Eldredge and Kropp 1985; Houk 2011). Consequently, coral cover and species richness are relatively low (Houk and Starmer 2010; Randall 1995) despite sufficient larval recruitment (Houk 2011; Randall 1985). Volcanic recurrence intervals of ~90 years were found most favourable for coral diversity in the archipelago. However, reef regeneration was slow with only 0.13% cover accretion and 0.21 newly settling species per year (Houk and Starmer 2010).

2.4.1. Mount Pagan

As one of the largest islands in the archipelago (Bearden et al. 2005; Houk and Starmer 2010), Pagan Island hosts the most diverse and abundant coral communities in the Northern Mariana Islands (Houk and Starmer 2010). The island is formed by two stratovolcanoes, Mount Pagan and South Pagan. The former accounts for most of the small to moderate (VEI 1-4) eruptions (Global Volcanism Program 2022). The largest event, a VEI 4 Plinian eruption in 1981 (Banks et al. 1984; Global Volcanism Program 2022; Henderson et al. 2019) produced tephra clouds reaching 13.5 km into the atmosphere and extending almost 1,000 km offshore (Guffanti et al. 2005). The material emitted during this event (Banks et al. 1984; Trusdell et al. 2005) locally accumulated to over 2 m in thickness. Most tephra was deposited into the surrounding ocean (Banks et al. 1984). Effusive lava flows from the 1981 eruption did not reach coastal waters (Eldredge and Kropp 1985).

Assessments of coral vitality and diversity undertaken two months prior to, two months after, and two years after the eruption in 1981 revealed spatially variant impacts from tephra fallout on coral communities in near-shore habitats. While all benthic biota was removed from zones of maximum deposition, protected coastal zones remained totally undamaged. These small-scale variations were attributed to local conditions in submarine relief and wave exposure: tephra fall impacts were lowest on elevated or vertical surfaces with high water circulation in

contrast to areas of flat seabed and low water movement where particles accumulated (Eldredge and Kropp 1985). Coral growth form and resultant sediment retention critically determined survival rates. Large colonies of massive *Porites* sp. were mostly unaffected, whereas open-canopy branching corals (e.g., *Acropora irregularis*) survived but exhibited stress symptoms. More compact branching coral (e.g., *Pocillopora elegans* and *Acropora tenuis*) were severely impacted by physical damage from tephra retained between branches. Post-eruptive mortality among *Pocillopora elegans* increased by ~40% within two years. Similar trends were detected for *A. tenuis* and *A. irregularis*. In areas of maximum deposition on the reef (up to 1 m), coral mortality from smothering was greater than 90%, with sporadic survivors located on elevated spots. Wave-induced erosion led to extreme water turbidity off the affected shorelines. Although these zones were not recolonized, rapid consolidation of volcanic materials to form solid silt layers on tephra beds was recognized. Despite scouring by floating ejecta with adverse effects on all biota in the intertidal zone, coral settlement occurred on solid submarine substrates. Benthic invertebrates were also killed by burial under deposits, albeit abilities to escape from affected zones increased survivorship. Macro-algae in shallow-water zones were effectively covered by tephra. In addition to reduced abundances, their diversity decreased by two thirds. Overall declines in marine species diversity and abundance were attributed to physical destruction and volcanically-induced habitat deterioration (Eldredge 1982; Eldredge and Kropp 1985).

Reef development around Pagan Island was limited by persistent disturbance and resultant harsh environmental conditions for coral. Consequently, minor recovery of coral cover and diversity was found ~25 years after the eruption in 1981 (Houk and Starmer 2010). Recent increased activity with ongoing degassing and tephra emission from April 2009 until December 2010 caused extensive coral mortality from rapid overgrowth by the coral-killing cyanobacterio-sponge, *Terpios hoshinota* in response to ocean water fertilization by iron enrichment. The reef returned to pre-eruptive state with coral dominance after volcanic activities ceased (Schils 2012).

2.4.2. Anatahan

Anatahan is a stratovolcano forming a small island (32.4 km²) in the Northern Mariana Islands (Bearden et al. 2005; Global Volcanism Program 2022; Nakada et al. 2005; Trusdell et al. 2005). Four eruption events (VEI 2-3) were reported between 2003 and 2008 (Global Volcanism Program 2022). Tephra emission from the first event in 2003, reached over 13 km

into the atmosphere (Guffanti et al. 2005; Hilton, Pallister, and Pua 2005; Trusdell et al. 2005). Ejecta covered more than half of the island's terrestrial surface (Chadwick et al. 2005) and tephra was transported more than 1,000 km away from the vent (Guffanti et al. 2005; Trusdell et al. 2005). Although deposition into the surrounding waters was not quantified (Lin et al. 2011; Trusdell et al. 2005), tephra fallout, sedimentation, and material resuspension were main hazards affecting Anatahan's near-shore coral reefs (Houk and Starmer 2010; Vroom and Zgliczynski 2011).

Benthic community assessments conducted four months after the eruption start in May 2003 revealed substantial reef damage from volcanic impacts. In zones of maximum deposition, deep tephra completely covered and effectively eliminated the entire benthos. The severity of observed biotic impacts reflected the local gradient of material deposition. In addition to smothering and sedimentation, localised turbid water plumes persisted for months (Bearden et al. 2005; Vroom and Zgliczynski 2011). Drastic declines in four functional groups of reef organisms were detected around Anatahan and the cover of live coral, crustose coralline red algae, and macroalgae was reduced by factors of 2.3, 1.4, and 3.0, respectively, in comparison to Sarigan, an unaffected island ~40 km to the northeast (Vroom and Zgliczynski 2011). Surviving corals of various genera (including *Favia*, *Goniastrea*, *Leptastrea*, *Montastrea*, *Montipora*, *Pavona*, *Platygyra*, *Pocillopora*, and *Porites*), invertebrates (e.g., *Polychaeta* and molluscs), and macro-algae were found at less affected reef sites. However, most surviving corals exhibited stress symptoms like bleaching. *Porites* sp. and *Goniastrea* sp. showed highest relative cover rates after the volcanic disturbance. The high abundance after the impact might be attributed to the initial dominance of *Porites* sp. (Vroom and Zgliczynski 2011), whereas adaptive strategies towards increased suspension feeding under limited light availability are documented for *Goniastrea* sp. (Anthony & Fabricius, 2000). Both genera are also able to remove sediments from their surfaces and tolerate temporary burial (Fabricius 2005), strengthening their resilience to recovery from tephra deposition. Crustose coralline algae also showed remarkable tolerance and survived for months despite coverage by volcanic deposits. Diversity and abundance of macroalgae in contrast, was drastically reduced (Vroom and Zgliczynski 2011). Similarly, turf algal communities declined by 50% (Tribollet and Vroom 2007).

In terms of habitat impacts, tephra deposition reduced availability and structural complexity of benthic reef habitats. Wave action could clear off sediments and mitigate ecological impacts at reef scale (Tribollet and Vroom 2007; Vroom and Zgliczynski 2011). However,

extreme hydrodynamics created unstable substrates and therefore little coral framework was found. In those areas, coral specimens were mostly juvenile *Porites* sp., *Pocillopora* sp., *Pavona* sp. and encrusting faviid corals (Houk and Starmer 2010).

2.5. Banda Api

Banda Api, and neighbouring islands Banda Neira and Banda Besar to the east and southeast, represent the rim of a mostly submerged caldera extending over 7 km in the north-east of the Sunda Arc in the Banda Sea, Indonesia. The steep tuff cone of 3 km in diameter peaks at an elevation of ~600 m (Global Volcanism Program 2022). Documented activities of small to moderate intensities (VEI 1-3) were mostly crater-building Strombolian eruptions dating back to the 16th century. The explosive events were associated with tephra emission and effusion of viscous andesitic lava (Casadevall, Pardyanto, and Abas 1989; Global Volcanism Program 2022; Pardyanto and Suratman 1991).

During the most recent eruption in 1988, three separate lava flows covered ~70,000 m² of benthic substrates along Banda Api's northern, north-eastern, and southern coastline (Casadevall et al. 1989; Heikoop, Tsujita, Risk, et al. 1996). Nearshore coral reefs were buried by lava reaching down to ~50 m below the surface (Sutarna 1990; Tomascik et al. 1996). In addition, tephra fallout from a plume of 3,500 m in height covered over 4.9 km² of coastal coral reefs on Banda Api's leeward western side. Material was deposited with mean and maximum thicknesses of 25 cm and 1 m, respectively, on land (Casadevall et al. 1989; Heikoop, Tsujita, Risk, et al. 1996; Pardyanto and Suratman 1991). In the impact area, tephra accumulated on coastal fringing reefs. Impact from both volcanic hazards on local coral communities ranged from absolute destruction to no detected effects (Heikoop, Tsujita, Risk, et al. 1996; Tomascik et al. 1996).

Benthic field surveys five years after Banda Api's eruption in 1988 revealed insights on hazard effects and ecological reef recovery. The lava flows had transformed the former coral reef into a structurally complex and stable benthic substrate free of predators or competitors suitable for new coral settlements. Adjacent to the lava flows, extreme water heating during the eruption affected coral communities (Tomascik et al. 1996); although the extent of thermally-induced coral die-off is not well delineated, extensive mortality in shallow water of 0-2 m depth and partial mortality of colonies at 2-4 m below the surface was observed in the impact zone (Tomascik et al. 1997). Reefs blanketed under tephra deposits but not covered by

lava were not completely destroyed, but live coral cover was reduced (Heikoop, Tsujita, Risk, et al. 1996; Tomascik et al. 1997). Mortality was caused by anoxia that stimulated microbial activity and enhanced bioerosion. Branching corals, such as *Acropora* sp. and *Pocillopora* sp., exhibited a higher susceptibility to material cover compared to compact growth forms. X-radiography of massive *Porites* skeletons revealed impacts from tephra fallout on the colonies and distinctive ferrous lines, the “Banda Band”, in their skeletons (Heikoop, Tsujita, Risk, et al. 1996). The latter anomalies coincide with the timing of the 1988 eruption and were linked to associated hydrothermal venting (Heikoop, Tsujita, Risk, et al. 1996). Tissue necrosis and enclosed tephra particles were also found at partial mortality surfaces (Heikoop, Tsujita, Risk, et al. 1996).

Around Banda Api, seawater acidification from continuous hydrothermal venting did not determine the coral community structure (Januar et al. 2017). Massive *Porites* sp., encrusting *Montipora* sp., and branching *Pocillopora* sp. were most abundant in areas of loose volcanic substrates, reflecting the resilience and adaptive abilities of these genera (Tomascik et al. 1997, 1996) whereas the dominant pioneers on sheltered lava flows were tabular *Acropora* sp. The rapid growth rates of these species accounted for the high overall coral cover on the stable and newly created benthic substrate (Tomascik et al. 1997, 1996).

After ~5 years, coral community diversity, species richness, abundance, and live coral cover on the northern lava flows were higher in comparison to nearby reef zones that were protected from lava influx or at locations where loose volcanic substrate remained (Tomascik et al. 1996). For example, 124 different species and an overall coral cover of over 60% were recorded at benthic communities on the recent lava flows, and the community included 35% of rare or uncommon species of *Acropora* (Tomascik et al. 1996). Overall richness and abundance of surrounding larvae refugia and the biogeographic setting were key factors for the formation of these local diversity hotspots (Tomascik et al. 1996). Such increase in local species richness might partially be attributed to niche generation for uncommon species indicating an intermediate state of succession prior to the onset of interspecific competition. In contrast, the recovering coral assemblages along the wave-exposed southwestern coastline remained in juvenile successional stage due to substrate instability from pyroclastic material deposition and ongoing erosion (Tomascik et al. 1996). This is a persistent pattern as indicated by a more recent reef assessment carried out on the lava flows where the coral reef was found in a very good condition with high overall cover rates and corals of different taxa present (Welly et al. 2012).

2.6. Rabaul

The Rabaul volcanic complex is located in the subduction zone between the Pacific, the South Bismarck, and the Solomon plates in north-eastern New Britain, Papua New Guinea (Finlayson et al. 2003; Global Volcanism Program 2022). The largely submerged caldera of around 10 by 15 km in extent was formed by distinct construction and collapse events over 3,500 and 1,400 years ago (Global Volcanism Program 2022; Heming 1974; McKee and Duncan 2016). The complex consists of five basaltic-andesitic cones of volcanic vents (McKee, Itikarai, and Davies 2017). To date, the two pyroclastic shields volcanoes “Tavurvur” and “Vulcan” are active and jointly account for recent eruptions (e.g., in 1878, 1937-1943, 1994-1995) (Global Volcanism Program 2022; McKee and Duncan 2016; Nairn et al. 1995). The complex’s overall eruption return rate over the past 250 years was estimated at around 24-60 years (McKee and Duncan 2016).

Ongoing seismic unrest within the caldera was noted for 23 years prior to a large Plinian eruption in 1994 (VEI 4). During this event, pyroclastic flows and base surges triggered tsunami waves up to 8 m high advancing up to 200 m inland in the Rabaul Harbour natural embayment. Among other fractions, pumice-rich tsunamites contained fragments of corals and shells (Nishimura et al. 2005). Seismic activities caused local coastal uplift by up to 6 m resulting in aerial exposure of benthic areas (McKee et al. 2017). Rapid local elevation changes of coral terraces were also reported in association with more recent activity in 1997 (Munday 2000). Uplifted and reworked coral reef limestones embedded in pyroclastic material date back over 0.125 Mya and indicate a long sequence of such tectonic reef disturbances in the region (Nairn et al. 1995).

In addition to local tephra accumulation of up to 90 cm (Blong 2003), the embayment of Rabaul Harbour, which is surrounded by the volcanic vents of the complex, was also filled with thick rafts of floating pumice following an eruption in 1994 (Nishimura et al. 2005) which smothered previously healthy coral reefs (50% coral cover; Maniwavie et al. 2001) within the bay. After two years, high density settlements of *Pocillopora* sp. from local populations were found on hard structures protruding from deep sediment beds on the reef flat. Whereas, zones of low relief with loose volcanic sediments were not recolonized (Maniwavie et al. 2001). Partially damaged colonies on reef slopes and outside the primary deposition zone regrew (Maniwavie et al. 2001) and evidence in an X-radiography of a massive *Porites lobata* core collected near Rabaul by Quinn, Taylor, and Crowley (2006)

reveals anomalous growth and apparent particle inclusion during 1994. After five years, live coral cover had returned to pre-eruption levels (Munday 2000). No documentation exists on the following development or potential impact of more recent volcanic activity (seven eruptions of VEI 1-4 from 2002 until 2014) on the coral reefs in Rabaul Harbour.

2.7. Piton de la Fournaise

Reunion Island in the western Indian Ocean is formed by two basaltic shield volcanoes, the inactive Piton des Neiges in the north and the active Piton de la Fournaise in the southeast (Global Volcanism Program 2022). Records of small to moderate (VEI 0-2) eruptions include tephra emission but the primarily hazard for local coral reefs is from lava effusion which has occasionally reached coastal waters over the past decades (Coppola et al. 2009; Michon et al. 2013). For example, during a caldera collapse event in 2007, lava ejected from fissures along the eastern flank formed a coastal delta of $\sim 0.52 \text{ km}^2$. This event of coastline propagation was associated with hydrovolcanic explosions due to the high material load and flow rate (Urai, Geshi, and Staudacher 2007). As newly formed volcanic materials are subjected to ongoing erosion, the island's eastern submarine flank is primarily characterized by unstable deposits of subaerially erupted lava, recurrent landslides, and subsidence to form turbidity currents (Labazuy 1996; Saint-Ange et al. 2013). Several records of distinct coral-bearing carbonate layers embedded in lava in Reunion Island and the neighbouring Mauritius dating from 0.26 million until 37,000 years ago indicate numerous of such past perturbations at volcanic sites in the Indian Ocean region (Montaggioni and Martin-Garin 2020).

Scattered coral reef formations along Reunion Island's south-eastern coast have been affected by the lava influx and in direct impact zones, mortality rates among benthic organisms were high (Bollard et al. 2012; Pinault et al. 2013, 2014). Coral communities on submarine lava flows of different ages showed clear differences in comparison to undisturbed reef sites with higher diversity and cover rates at unaffected sites (Jouval et al. 2020). The suppression of species richness in recovering communities was attributed to adverse habitat conditions (Jouval et al. 2020), including dark volcanic substrates to limit light available to benthic photo-symbionts (Schleyer et al. 2016) and soft sediments that are unsuitable for coral settlement. Opportunistic *Pocillopora* sp. were dominant pioneers on flows, but over years to decades, species numbers increased with longer lava influx recurrence (Jouval et al. 2020; Pinault et al. 2013, 2014). Similarly, higher diversity and density of sponges, octocorals, ascidians, and echinoderms was recognized on older flows compared to younger ones

(Bollard et al. 2012; Schleyer et al. 2016). In contrast, endemism and diversity of fish communities was elevated on young lava flows due to new niche generation by volcanic perturbations (Pinault et al. 2013, 2014).

2.8. Kīlauea

Similar to Reunion Island, Hawaii is an oceanic volcanic hotspot. Currently, Kīlauea is the most active vent in the archipelago on the Pacific plate (Global Volcanism Program 2022; Moore and Clague 1992). With a caldera of 3 by 5 km in extent, the basaltic shield volcano covers the eastern flank of Mauna Loa on the Island of Hawaii along a rift zone from summit to coast (Global Volcanism Program 2022; Stearns 1926). Ninety percent of the volcano's surface material is younger than 1,100 years (Holcomb 1987). Thus, many lava flows have been emplaced onto the edifice and occasionally enter coastal waters (Moore et al. 1973). Documented activities include caldera collapse associated with explosive eruptions of variant intensities. Ongoing long-lasting basaltic lava extrusion covered over 100 km² and contributed to frequent coastline propagation (Global Volcanism Program 2022; Holcomb 1987; Stearns 1926).

In the Hawaiian archipelago, reef growth along the volcanically-affected shores was limited by lava influx during the volcanic stage of shield formation ~130-465 ka, whereas stable habitat conditions promoted sustained coral development and formation of coastal fringing reefs (Dana 1872; Holcomb 1987; Moore 1970; Moore and Clague 1992). However, due to the archipelago's isolated location in the central North Pacific at the extreme of larval dispersal pathways, recruitment of coral reef species from external sources is limited (Jokiel 2008) and overall coral diversity is relatively low (~40 species of stony corals) (Maragos 1995). Drowning coral reefs due to edifice subsidence from high crustal lithospheric loads have been reported from the Hawaiian archipelago (Jones 1995; Moore and Clague 1992).

While lava influx in coral reef habitats typically annihilates any benthic biota, it can also lead to the establishment of new uncolonized basalt surfaces (Grigg and Maragos 1974; Jokiel 2008). At six sites of different flow ages (1.6-102 years) along the southern coastline of Hawaii, highest coral diversity was found at intermediate volcanic disturbance frequency of around 45 years. Species numbers initially increased but declined with the onset of interspecific competition. Following burial by lava, perturbations from wave impacts

constrained coral community development at incipient levels, whereas more complex and species rich assemblages formed without continuous disturbances (Grigg and Maragos 1974).

Species-specific tolerance and recovery characteristics were recognized: *Pocillopora* sp. were dominant first colonisers on lava flows whereas *Montipora verrucosa* for example, only settled after several years. Colonies of *Porites lobata* and *Pocillapora meandrina* that had been partially submerged by lava flows were observed to continue to grow from the surviving emergent parts of the colony within just centimetres away from the flow margins (Grigg and Maragos 1974; Moore et al. 1973). Despite very high core and margin flow temperatures of over 1,000°C (Pinkerton, James, and Jones 2002), only slight increases in water temperature of around 2.5°C were recorded in close proximity (< 10 cm) to slow-moving submarine lava (Moore et al. 1973). During earlier events, fish die-off associated with lava entry was observed (Dana 1872; Gosline et al. 1954). Submarine outcrops provided protection for benthic organisms and intact reef patches with unaffected and large coral colonies, mobile benthic invertebrates, and reef fish were found (Moore et al. 1973).

2.9. Soufrière Hills

Located in the subduction zone between the Atlantic and the Caribbean Plate, Montserrat is part of the Lesser Antilles volcanic arc. Soufrière Hills is the youngest of the islands four volcanic centres formed by five andesitic lava domes. Following three years of seismic unrest, volcanic activities started in 1995 for the first time after centuries of quiescence (Global Volcanism Program 2022; Robertson et al. 2000; Sparks and Young 2002). During the following 14 years, more than 1 km³ of andesitic lava was produced (Wadge et al. 2010). The activities were characterized by volcano-tectonic earthquakes, episodic events of lava dome growth and collapse mostly in association with Vulcanian or sub-Plinian explosions, tephra emission, and flank failure (Druitt and Kokelaar 2002; Global Volcanism Program 2022; Robertson et al. 2000; Wadge et al. 2014; Young et al. 1998). With pyroclastic flows being a major hazard in Montserrat with over 75% of the erupted volume transported into the sea between 1995 and 2005. Coastal deltas and submarine fans formed at river mouths along the south-eastern and western coastline (Le Friant et al. 2009; Trofimovs et al. 2008). Furthermore, tephra deposition into surrounding waters and pyroclastic pumice rafts were reported (Druitt and Kokelaar 2002; Trofimovs et al. 2008).

Pyroclastic material sedimentation and continuous terrestrial erosion impaired Montserrat's coastal coral reefs (Myers 2013; Spalding et al. 2001). Perturbations at reef-scale were most extreme along the volcanic flanks on the eastern and western coastlines where coral reefs were frequently covered (Carey et al. 2014). Apart from breakage and burial, fragments of benthic biota, including corals, foraminifera, gastropods, and bryozoans were displaced and eroded off the shelf (Fisher et al. 2008). Consequently, widely distributed biogenic carbonate fragments account for up to 5% of the deep sea deposits (Trofimovs et al. 2008). However, sedimentation impacts decreased with distance from terrestrial run-off zones and were mitigated by waves and currents to reduce coastal sediment retention (Carey et al. 2014). Reflecting those patterns, reef zones in the north and south of Montserrat remained intact hosting diverse communities of benthic biota. Like reported from other volcanic sites, coral communities developed on volcanic substrates (Myers 2013). However, no studies on coral reef recovery around Soufrière Hills have been published.

2.10. Hunga Tonga–Hunga Ha’apai Island

Located in the Tonga-Kermadec volcanic arc, around 770 km southeast of Fiji in the southern Pacific Ocean, Hunga Tonga–Hunga Ha’apai Island (HTHH) is formed by outcrops of a mostly submerged caldera that originates from volcanic activities in 1040-1180 CE (Brenna et al. 2022). Multiple submarine eruptions occurred since the first reported event in 1912. New land from volcanic deposits that were added in 2009 and 2014-2015 was subject to ongoing marine erosion. Individual volcanic outcrops were connected by a circular tuff cone of unconsolidated andesitic deposits (Garvin et al. 2018; Vaughan and Webley 2010) prior to a series of explosive eruptions in 2021-2022 that reshaped the geomorphological structure. During the last activity in 2022, an eruption plume up to more than 50 km was emitted into the atmosphere (Carr et al. 2022), pressure waves, and a tsunami in the southern Pacific Ocean were triggered (Global Volcanism Program 2022). For past and recent Surtseyan eruptions at HTHH, increased water turbidity, formation of floating pumice rafts, and anomalies sea surface temperatures were documented (Global Volcanism Program 2022; Shi and Wang 2011; Vaughan and Webley 2010).

Although Shi and Wang (2011) did not focus on coral reefs, they noted their vulnerability to proximal submarine eruptions in Tonga by adverse habitat conditions (Shi and Wang 2011). Observations of dead fish and birds in the impact zone of the VEI 2 event at HTHH in 2009 indicate susceptibility of marine organisms to hydro-magmatic activities (Vaughan and

Webley 2010). Ecological reef surveys in 2018 showed that despite the small island size (maximum southeast-northwest extension 3.5 km), the moderate VEI 2 event in 2014-2015 did not fully destroy all coral reefs but caused spatially variant impacts. Smothering by tephra and sedimentation of pyroclastic materials, water turbidity, and water heating effectively obliterated benthic communities at exposed shorelines. In contrast, topographically protected reefs exhibited high coral species richness and live cover after four years. Here, surviving *Acropora* sp., *Pocillopora* sp., and *Porites* sp. showed neither stress symptoms, nor growth limitations (Smallhorn-West et al. 2020). Contrarily, high mortality rates and cover reductions characterized reef sites exposed to the volcanic impacts where only individual massive *Porites* sp. colonies survived but exhibited extensive partial necrosis. Their skeletal structures showed stress bands and particle inclusions (Smallhorn-West et al. 2020). Impact patterns on reef fish assemblages in terms of biomass and diversity were similar to observed disturbances to coral communities and reflected spatial gradients of impact exposure (Smallhorn-West et al. 2020).

High coral recovery rates of ~45% within less than four years, with generically diverse and abundant juvenile colonies at sites formerly covered by deposits during events in 2014-2015 were documented (Hite et al. 2020; Smallhorn-West et al. 2020). Such quick successional development was attributed to self-recruitment of fast-growing *Acropora* sp. and *Pocillopora* sp. from persistent local refugia and the lack of additional stressors (e.g., human interventions). By 2018, diverse coral communities had re-established within four years following volcanic perturbations (Smallhorn-West et al. 2020). No reef assessment has been undertaken since the latest explosive eruption from December 2021 until January 2022.

2.11. Conclusion and future perspective

By covering all tropical coral reef provinces and including different volcano-tectonic settings, a variety of volcanological hazards under different environmental conditions at reef scale is accounted for. Despite the site-specific character of each case study, unifying patterns of volcanic impacts on coral reef ecosystems emerge from the compiled records. Those general trends are outlined and evaluated in the following sections of this thesis. Most of the included studies provide baseline records on volcano-reef-interrelations (e.g., for Anatahan by Vroom and Zgliczynski 2011). However, the value of continuous and follow-up analyses tracking coral reef development subsequent to volcanic impacts is evident (e.g., for Rabaul by Maniwavie et al. 2001). More detailed and standardized ecological assessments of coral reefs

exposed to volcanism would improve future understanding. In particular, long-term records providing pre- and post-disturbance information would support the description of volcanism as a natural disturbance regime to coral reefs.

Table 2.21: Summary of reported changes to coral reefs detailed in case studies. Refer to tab. 2.1 for full references.

Volcano	Changes to coral reef	Primary volcanic driver	Relative reef state prior to direct volcanic impacts
Krakatau	Live coral cover loss, changed coral reef distribution, dislocation of coral fragments, interruption of coral reef development, species turn-over	Burial under deposits, heavy wave impacts, ongoing material deposition	Incipient successional stage, rapid coral reef changes
Pinatubo	Live coral cover reduction, coral growth stop, algal overgrowth, loss of other reef-associated species	Smothering from sedimentation, changes in habitat conditions (substrate and water), eutrophication	Species-rich coastal fringing coral reefs in direct impact zone and distal reefs affected by eutrophic conditions
Mount Pagan	Local elimination of coral reef, selective species decimation determined by growth form, stress symptoms, reduced species diversity, loss of other reef-associated species	Smothering from material fallout and ongoing sedimentation, trophic changes	Relative higher species diversity and live coral cover
Anatahan	Live coral cover reduction, loss of other reef-associated species, stress symptoms, changes in coral species composition	Smothering from material deposition	Higher live coral cover
Banda Api	Live coral cover loss, partial to complete coral reef elimination, (temporarily) elevated coral diversity	Material deposition by lava influx and tephra fallout	Well-developed coral reefs of medium diversity shaped by competition and controlled by adverse habitat conditions
Rabaul	Live coral cover reduction, changed coral reef distribution	Smothering from material deposition, abrasion	High coral reef biodiversity
Piton de la Fournaise	Reduced species diversity, abundance and live coral cover change; altered species composition	Lava influx	Higher coral diversity
Kilauea	Limited coral reef development, species turn-over	Lava influx	Coral diversity changes with successional recovery
Soufrière Hills	Cover losses, dislocation of coral fragments and other reef-associated organisms	Coastal material deposition	Diverse coral communities, low overall coral cover
Hunga Tonga–Hunga Ha’apai	Local coral reef elimination, live coral cover reductions, stress symptoms,	Material deposition and removal by eruption blast	Species-rich pristine coral reef communities

3. Chapter 3 – Patterns of volcanic impacts on coral reefs

3.1. Introduction

The destructive potential of volcanic activities exceeds the disruptive effects of most natural disturbances to coral reef ecosystems. Reef organisms may not only be directly impacted by eruptive products, but habitat conditions can be altered from local to global scales (Tomascik et al. 1996). Burial by pyroclastic materials can significantly affect reef-associated biota (Maniwavie et al. 2001). Whereas impacts directly associated with eruptions may be temporally constrained and limited in spatial extent, subsequent follow on consequences in terms of altered environmental habitat conditions continue to directly and indirectly impact on coral reefs, well beyond the period of active volcanism (e.g., Reuter and Piller 2011; Tomascik, van Woelik, and Mah 1996; Vroom and Zgliczynski 2011). Contrasting the destruction of reef organisms, volcanic bedrock forms the base for coral reef generation and thus enables species proliferation and community development (Darwin 1842; Piller and Riegl 2003; Sluiter 1890; Smallhorn-West et al. 2020).

This section consists of a review of volcanic impacts on coral reefs. Table 3.1 contains a summary with impacts grouped into either direct or indirect impacts and respective effects on coral reef organisms with key references for examples presented in the literature. To aid understanding, the different impact types are illustrated in schematic summaries of impacts (Fig. 3.1) and volcanic drivers as well as reported biotic reef responses are outlined in detail.

Table 3.1: Overview of direct and indirect volcanic impacts and their effects on coral reef organisms and ecosystems.

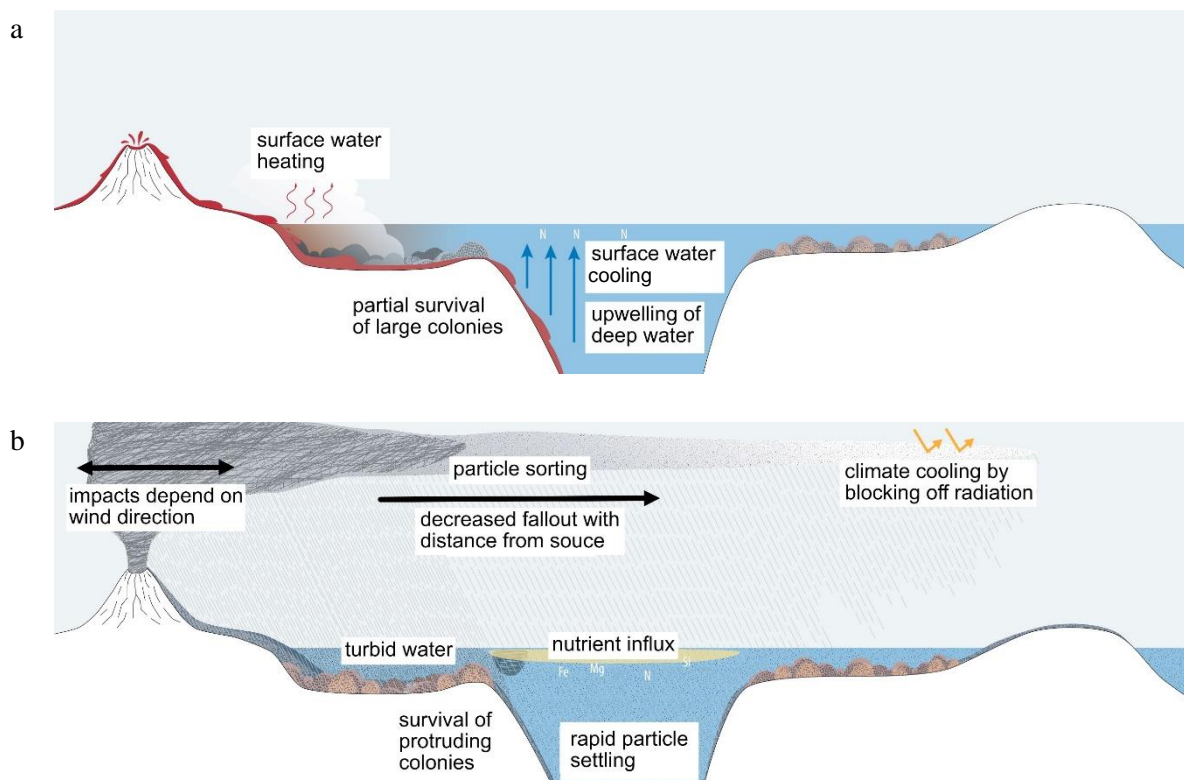
Volcanic impacts	Effects on coral reef organisms	Time	Spatial extent	Severity	Selected references
Direct impacts					
Lava flow, pyroclastic material deposition	Burial, skeletal fracture, dislocation, stress symptoms (e.g., bleaching), heat stress, habitat loss, (partial) necrosis, mortality	Days to months	Local (> 10 km)	Fatal	Bearden et al. 2005; Bollard et al. 2012; Fisher et al. 2008; Grigg and Maragos 1974; Houk 2011; Montaggioni and Martin-Garin 2020; Mutaqin 2020; Mutaqin et al. 2019; Pinault et al. 2013, 2014; Reuter and Piller 2011; Smallhorn-West et al. 2020; Spalding et al. 2001; Tomascik et al. 1997, 1996; Trofimovs et al. 2006; Wilson and Lokier 2002
Pyroclastic density current, lahar, tephra fall	Burial, skeletal fraction, dislocation, growth anomalies, particle inclusion, stress	Days to months	Local to regional (up to 1,000 km)	Minor damage up to complete elimination	Atrigenio et al. 1991; Bearden et al. 2005; Eldredge 1982; Eldredge and Kropp 1985; Heikoop, Tsujita, Heikoop, et al. 1996; Houk 2011; Houk and

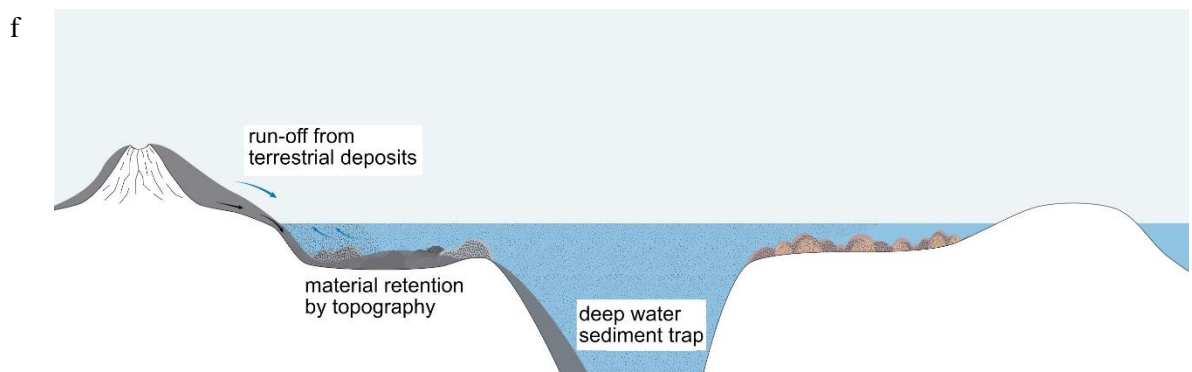
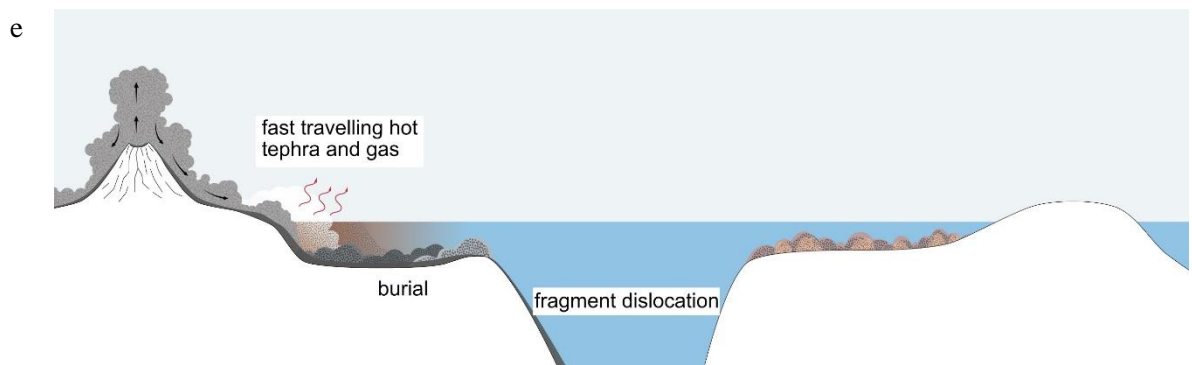
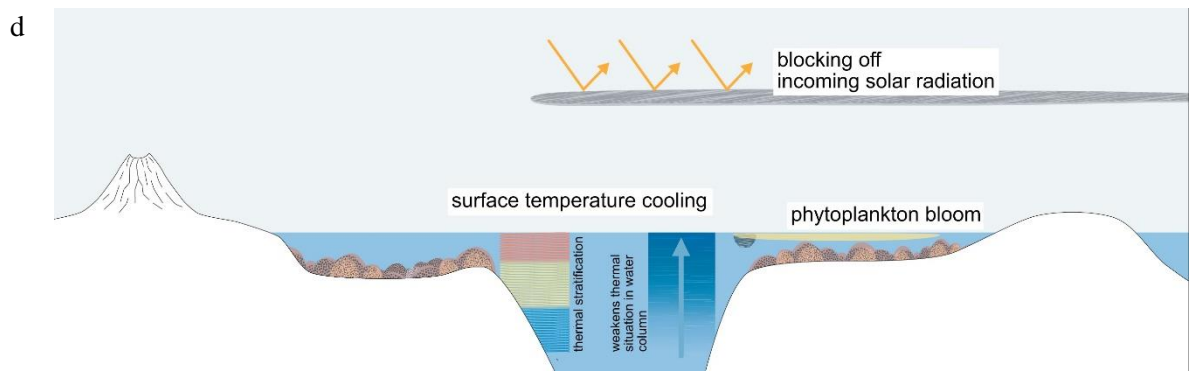
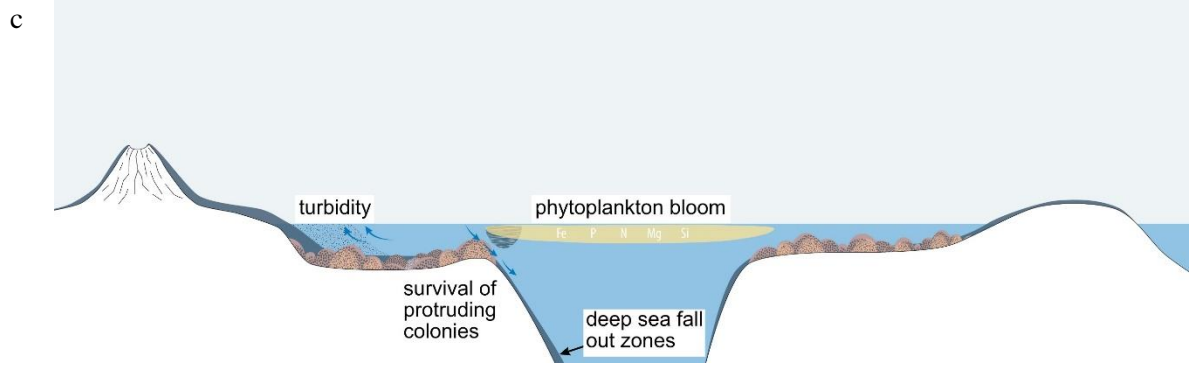
	symptoms (e.g., bleaching), nuisance species spread, food scarcity, habitat loss, disorientation, (partial) necrosis, mortality				depending on intensity	Starmer 2010; Maniwavie et al. 2001; Mutaqin 2020; Ochavillo et al. 1992; Ono, Reimer, and Tsukahara 2002; Pajaro et al. 1992; Pandolfi et al. 2006; Reuter and Piller 2011; Schils 2012; Tomascik et al. 1997, 1996; Tribollet and Vroom 2007; Vroom and Zgliczynski 2011; Witt et al. 2017; Wu et al. 2018; Yamashiro and Fukami 2012
Drifting pumice	Remove, scouring	Days to years	Local to continental (up to 10,000 km)	Partial destruction	Eldredge and Kropp 1985	
Uplift or subsidence, volcanogenic earthquakes	Aerial exposure, reef drowning	Millenia	Local (< 10 km)	Fatal	Chen et al. 1995; Jones 1995; Moore, Normark, and Szabo 1990; Yao et al. 2013; Zhan et al. 2006	
Indirect impacts						
Sedimentation of unconsolidated (terrestrial and marine) volcanic deposits	Burial, dislocation, fraction, anomalies, necrosis, mortality	Days to decades	Local (< 10 km depending on topography)	Partial destruction	Houk and Starmer 2010; Jones 2015; Smallhorn-West et al. 2020; Trofimovs et al. 2006; Wilson and Lokier 2002	
Water turbidity, suspended sediment, reduced light penetration	Growth and productivity reduction, limited productivity, community compression in photic zones, photo-symbiont die-off, mortality	Days to years	Local to regional (< 100 km)	Partial destruction	Atrigenio et al. 1991; Barber et al. 2002; Bearden et al. 2005; Eldredge 1982; Eldredge and Kropp 1985; Gagan et al. 2015; Genin et al. 1995; Houk 2011; Reuter and Piller 2011; Schleyer et al. 2016; Smallhorn-West et al. 2020; Umbgrove 1930; Vroom and Zgliczynski 2011; Wilson and Lokier 2002; Wu et al. 2018	
Chemical water alterations (pH and salinity variations, pollution, nutrient and toxin influx)	Species changes, composition, nuisance species spread, algal overgrowth, poisoning, mortality	Days to years	Local to regional (< 100 km)	Partial destruction	Houk and Starmer 2010; Reuter and Piller 2011; Schils 2012; Wilson and Lokier 2002	
Eutrophication	Algal overgrowth, anoxia, trophic phase-shift (from coral to algae dominance), mortality	Days to years	Local to regional (< 100 km)	Partial destruction	Genin et al. 1995; Schils 2012	
Water heating	Bleaching, (partial) necrosis, mortality	Days to weeks	Local (< 10 km)	Partial destruction	Dana 1872; Gosline et al. 1954; Grigg and Maragos 1974; Moore et al. 1973; Sigurdsson et al. 1991; Smallhorn-West et al. 2020; Tomascik et al. 1996	
Habitat generation	Creation of stable benthic substrates, facilitation of dispersal, temporary exclusion of predators and competitors	Years to decades	Local (< 10 km)	No destruction	Bearden et al. 2005; Darwin 1842; Houk and Starmer 2010; Piller and Riegl 2003; Pinault et al. 2013, 2014; Sluiter 1890; Smallhorn-West et al. 2020; Spalding et al. 2001; Terry and Goff 2013; Tomascik et al. 1996	

3.2. Direct volcanic impacts

3.2.1. Material deposition

Direct impacts of volcanic activity on coral reef ecosystems are primarily caused by volcanoclastic material deposition resulting from hazards such as pyroclastic density currents, lahars, tephra fallout, and lava flows (Tab. 3.1). Burial from material deposition can cause physical damage and high mortality rates among reef biota (Reuter and Piller 2011). Such smothering is commonly associated with a range of hazards from volcanic activities including lava flows (Fig. 3.1 a), tephra deposition (Fig. 3.1 b), pyroclastic density currents (Fig. 3.1 e), or hydro-magmatic activities (Fig. 3.1 h). Reef organisms may also be buried under reworked volcanic deposits. This concerns erosion of unconsolidated volcanic material (Fig. 3.1 f), and landslides (Fig. 3.1 g) into coastal coral reef habitats. Depending on eruption type and intensity, multiple direct hazards can occur in parallel. For example, material deposition from cone collapse (Sluiter 1890), submarine pyroclastic density currents (Mandeville et al. 1994), pumice, and tephra deposition cleared the benthic zone within 15 km around the Krakatau volcanic complex in 1883 (Carey et al. 1996; Mandeville et al. 1996; Simkin and Fiske 1983).





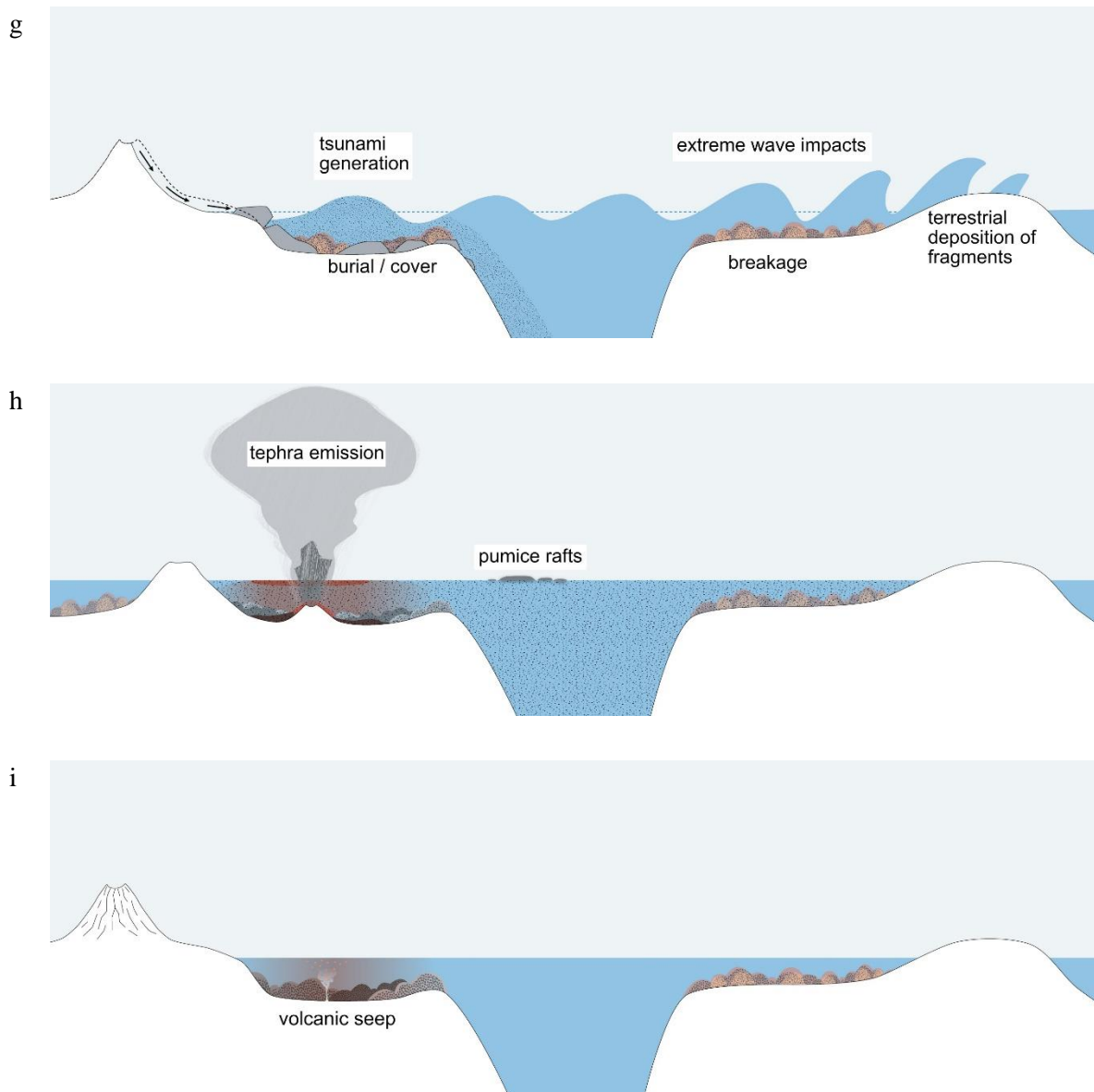


Figure 3.1: Schematics of impacts on coral reefs from different volcanic hazards during eruptive periods: a) lava influx, b) direct impacts from tephra deposition, c) indirect impacts from tephra deposition, d) climatic impacts from sulphate aerosol generation in the stratosphere, e) pyroclastic influx, f) erosion of unconsolidated deposits, g) landslides and tsunami generation, h) Surtseyan eruption, and i) hydrothermal venting. Changes over time can be deduced by comparing this depiction with fig. 4.1. Illustrations created by Nguyen Thi Nam Phuong, Earth Observatory of Singapore.

While escape behaviour prior to volcanic activities has been observed in some marine animals (Mendoza, Clemente, and Hernández 2020), reef fish and most benthic organisms, including scleractinian corals, are constrained at local habitat scale and thus affected by the impacts of volcanic material deposition (Ochavillo et al. 1992; Tomascik et al. 1996). In corals, species-specific resilience to sediments in general has been correlated with growth form and colony size (Eldredge and Kropp 1985; Vroom and Zgliczynski 2011). Impact severity is also determined by sediment rejection abilities (Duckworth, Giofre, and Jones

2017; Fabricius 2005), adaptations of feeding strategies (Anthony and Fabricius 2000), and physiological tolerance levels (Fabricius 2011; Tuttle and Donahue 2022). Physical damage from burial, dislocation, skeletal breakage, tissue injuries, and necrosis may only cause partial mortality of a coral colony. Unaffected branches, protected from direct impacts or protruding out of the deposition horizon, can maintain living polyps (Eldredge and Kropp 1985; Heikoop, Tsujita, Risk, et al. 1996; Vroom and Zgliczynski 2011). High overall abundance was recognized to enhance survival of respective species (Pandolfi et al. 2006; Vroom and Zgliczynski 2011). A certain degree of mobility allows other reef organisms, such as benthic foraminifera, to self-extract from sediments (Alve 1999).

In the path of lava flows entering coastal waters (Fig. 3.6 a), scleractinian corals and other benthic organisms may partially or entirely be covered by the flow material (Dana 1872; Grigg and Maragos 1974; Tomascik et al. 1996). Although lava influx is an acute disturbance (Graham, Nash, and Kool 2011), the impact is limited in spatial extent within a few kilometres (Perfit and Soule 2016) and locally constrained by topographic features (Bollard et al. 2012). Elevated locations within the reef matrix provide protection from the impact (Moore et al. 1973) and form substrate for subsequent settlement (Königshof, Nesbor, and Flick 2010). Carbonate units interbedded with lava deposits indicate recurrence of burial and resettlement sequences. In the western Indian Ocean, three facies coral deposits dating back 0.28 Mya were found in Reunion Island (an active volcano). In Mauritius, another volcanic island, geological records show seven carbonate facies from the late Miocene until ~120,000 years ago (Montaggioni and Martin-Garin 2020). Similarly, material deposition from pyroclastic density currents can smother, damage, and dislocate benthic organisms, as evident following volcanic events along the Sunda Arc (Mutaqin 2020; Mutaqin et al. 2019) and in the Caribbean (e.g., Soufrière Hills on Montserrat) (Fisher et al. 2008). Coral fragments from coastal reefs in Montserrat were carried off the shelf for over 30 km and deposited among other debris (Trofimovs et al. 2006). In general, high material transport rates and continuous influx reduces local coral reef development (Mutaqin et al. 2019; Spalding et al. 2001).

Tephra deposition from explosive eruptions is a far-reaching direct volcanic disturbance to coral reef ecosystems (Heikoop, Tsujita, Heikoop, et al. 1996; Reuter and Piller 2011; Vroom and Zgliczynski 2011; Witt et al. 2017). Volcanic ash, defined as the fraction of tephra < 2 mm in diameter, can travel over hundreds of kilometres from vent before fallout (Sparks 1986). Ground accumulation is typically determined by eruption type and magnitude, which

influences the height to which tephra is ejected, grain sizes and densities, as well as wind patterns during activity periods (e.g., Bonadonna et al. 2015; Casadevall et al. 1989; Jenkins et al. 2015). Accordingly, impacts vary from no detectable deposition to complete burial of benthic communities (Fig. 3.1 b). Such gradients were observed within single island surveys at Banda Api and in Anatahan following eruptions in 1988 and 2003, respectively (Tomascik et al. 1996; Vroom and Zgliczynski 2011). However, significant impacts at reef scale were mainly reported in close proximity (within < 10 km) from the volcano (Eldredge 1982; Eldredge and Kropp 1985; Heikoop, Tsujita, Risk, et al. 1996; Vroom and Zgliczynski 2011). A disturbance horizon of 16 cm tephra deposits on fringing reefs was reported from Pagan's eruption in 1981 (Eldredge 1982; Eldredge and Kropp 1985). The eruption of Banda Api in 1988 resulted in 25 cm deposition on average with maximum deposits of up to 1 m on the coastal reefs (Heikoop, Tsujita, Risk, et al. 1996). Such material fallout can rapidly bury coral reefs (Heikoop, Tsujita, Risk, et al. 1996; Maniwavie et al. 2001; Reuter and Piller 2011; Tomascik et al. 1996; Vroom and Zgliczynski 2011) and cover extensive coastal zones. For example, tephra fallout smothering coastal coral reefs over ~16 km was reported from Huon Peninsula in Papua New Guinea (Pandolfi et al. 2006).

Effects of tephra deposition on benthic organisms include smothering, tissue destruction, skeletal breakage, and abrasion (Eldredge and Kropp 1985; Pandolfi et al. 2006; Reuter and Piller 2011). Furthermore, sharp angular volcanic glass shards harm coral polyps when ingested (James and Kendall 1992; Wilson and Lokier 2002). Those physical impacts can induce adverse cascading effects, such as bioerosion, fouling, and elevated microbial activities on necrotic tissue (Heikoop, Tsujita, Risk, et al. 1996; Hodgson 1990). In consequence, coral reefs can be severely damaged from tephra fallout with up to 100% mortality (Maniwavie et al. 2001; Pandolfi et al. 2006). Trends of greater tephra deposit thickness causing higher rates of live coral cover reduction have been documented in different instances at Anatahan, in Rabaul Harbour, in Kagoshima Bay, and along the western coast of Zambales (Atrigenio et al. 1991; Maniwavie et al. 2001; Ochavillo et al. 1992; Ono et al. 2002; Pajaro et al. 1992; Vroom and Zgliczynski 2011). Abundance and diversity of other functional coral reef groups including fish and marine macroalgae was found similarly sensitive to volcanic material fallout (Ochavillo et al. 1992; Tribollet and Vroom 2007; Vroom and Zgliczynski 2011). Disorientation, habitat loss, and food scarcity were reasons for fish biomass declines along the western Philippine coastline following Pinatubo's eruption in

1991 (Ochavillo et al. 1992). Here, reduced fish biomass and live coral cover decline correlated (Pajaro et al. 1992).

Drifting pumice can also physically damage or even remove reef biota by scouring under the influence of wave energy (Eldredge and Kropp 1985). However, attached to rafting volcanoclastic materials, like pumice, a great variety of marine organisms including corals, may expand natural dispersal ranges (Bryan et al. 2012). Therefore, such floating material can effectively facilitate long-distance proliferation of marine organisms (Jokiel 1990) with potential implications on biodiversity patterns and altered connectivity between distant reef habitats. That way, attached organisms may even bypass natural barriers, like large oceanic basins (Lokier et al. 2009).

High vertical settling rates and accurate preservation of grain size distributions throughout the water column indicate minor oceanographic impacts on open ocean tephra sedimentation (Kandlbauer, Carey, and Sparks 2013; Wiesner et al. 1995). In contrast, due to the small particle size of fine tephra fractions, these deposits are often subject to hydrodynamic reworking and remobilization in more energetic coastal zones (Ono et al. 2002; Vroom and Zgliczynski 2011). Reef exposure to wave action can therefore mitigate the impacts of tephra deposition on benthic biota by clearing off sediments (Vroom and Zgliczynski 2011). However, this may as well induce water turbidity from ongoing resuspension of sediments (Houk and Starmer 2010; Reuter and Piller 2011).

3.3. Indirect volcanic impacts

3.3.1. Substrate stability

Material influx and sedimentation, particle resuspension, and ongoing terrestrial and marine erosion hamper reef formation (e.g., Trofimovs et al., 2006; Vroom & Zgliczynski, 2011). Along steep slopes of volcanic islands and watersheds, rapid erosion of unconsolidated material, landslides, or even flank collapse can cause downstream material deposition into coastal reef zones with implications on coral health (Barber et al. 2002; Chen et al. 1995; Houk and Starmer 2010; Pandolfi et al. 2006; Sluiter 1890; Smallhorn-West et al. 2020; Umbgrove 1930) (Fig. 3.1 f). Such sedimentation results from terrestrial run-off (e.g., Fabricius, 2005), siltation by rivers (Atrigenio et al. 1991; Mutaqin 2020; Ochavillo et al. 1992; Wu et al. 2018), and coastal wave exposure (Barber et al. 2002; Piller and Riegl 2003; Tomascik et al. 1996). Additional influx paths include aerial fallout and superficial material

transport on the ocean surface (Wilson and Lokier 2002). Apart from alterations to water chemistry and trophic state (Duggen et al. 2007; Wu et al. 2018), impacts on coral reef organisms primarily result from changed light and substrate conditions. Increased particle load, water turbidity, changes in bathymetry and reef substrate characteristics are potential consequences that affect critical habitat parameters of coral communities (Wilson and Lokier 2002).

Reworking and ongoing sedimentation of volcanoclastic materials from terrestrial into maritime systems may occur over millennia following particular eruption events (Kataoka, Urabe, and Nagahashi 2016). Magnitudes of such subsequent material transport typically exceed deposition rates of direct impacts and may be effective in distal coastal or pelagic zones from the volcano (Kataoka et al. 2009; Wu et al. 2018). In proximity to shore, high rates of sedimentation are associated with the formation of submarine turbidity currents (Bavestrello et al. 2014; Trofimovs et al. 2006). Material redeposition from land to reef zones can be enhanced by heavy precipitation and volcanically-induced removal of stabilizing vegetation to constrain sediment retention capacities within watersheds (e.g., Bavestrello et al., 2014; Eldredge, 1982; Groombridge et al., 2003; Smallhorn-West et al., 2020). Preferential coral settlement on solid ejecta in the form of lava flows and coarse but stable volcanic substrate versus lack of recovery in areas of fine-particulate unstable material in gullies was documented in Bali. Here, abrasive and erosive effects from loose material and boulders destroyed regenerated reef patches when mobilized by strong wave activity (Piller and Riegl 2003).

Topography (Maniwavie et al. 2001), site-specific wave exposure (Eldredge 1982; Eldredge and Kropp 1985; Heikoop, Tsujita, Heikoop, et al. 1996; Ono et al. 2002), and local water circulation (Atrigenio et al. 1991; Ochavillo et al. 1992) control sediment retention within a reef and determine organism-scale impacts (Houk and Starmer 2010; Vroom and Zgliczynski 2011). Elevated locations (Barber et al. 2002; Huang et al. 2018; Wilson and Lokier 2002) and vertical surfaces (Maniwavie et al. 2001) as well as sites of moderate wave influence favour coral survival by limiting retention of deposits and providing protection from burial under sediments. In comparison, flat reef zones and areas characterized by calm hydrodynamic conditions, form less suitable habitat under sediment influence with corals being more severely impaired by burial and unstable substrate (Eldredge 1982; Eldredge and Kropp 1985; Ono et al. 2002). Wave exposure may clear off fine-grained sediments (Reuter

and Piller 2011) and thus enable rapid recolonization (Vroom and Zgliczynski 2011), or contrarily induce continuous particle resuspension (Harper, Scrutton, and Williams 1995; Houk and Starmer 2010; Reuter and Piller 2011; Wilson and Lokier 2002), which prohibits substrate stabilization (Piller and Riegl 2003) and increases water turbidity (e.g., Mutaqin, 2020). Both factors can inhibit reef framework development (Piller and Riegl 2003) and consequently hamper coral recovery over prolonged time scales (Bearden et al. 2005; Heikoop, Tsujita, Heikoop, et al. 1996; Pandolfi et al. 2006). Increasing coral mortality over the course of two years after tephra deposition on the coastal coral reefs around Pagan Island (Eldredge and Kropp 1985) is most likely to be attributed to sustained adverse habitat conditions preventing rapid recovery.

Substrate stability is elementary to coral growth and recolonization (Grigg and Maragos 1974; Maniwavie et al. 2001; Starger et al. 2010; Tomascik et al. 1996). Unconsolidated sediments, such as loose tephra beds, inhibit coral recolonization whereas post-disturbance settlements on hard structures, like volcanic boulders, wooden debris, and coral fragments, can form rapidly (Maniwavie et al. 2001). However, over time, deep volcanic tephra deposits can consolidate on the seafloor to form marl and tuff layers, as found at Pagan Island (Eldredge and Kropp 1985; Heikoop, Tsujita, Heikoop, et al. 1996). This diagenetic cementation is promoted by organic matter decomposition (Reuter and Piller 2011). Such stable bases are suitable for coral recolonization. In the Northern Mariana Islands, erosion of loose volcanic material along steep slopes hampered reef development resulting in sporadic formations and failed coral settlement (Houk and Starmer 2010). Here, substrate types were found determining coral growth. Low rugosity substrates were found hosting less diverse coral assemblages and reduced individual colony sizes in comparison to volcanic boulders with intermediate, and primary reef framework with high levels of species richness and colony sizes (Houk and Starmer 2010). Also, benthic habitats are modified by volcanoclastic inputs in terms of their structural complexity and an increased ratio of abiotic surfaces (Vroom and Zgliczynski 2011).

However, initial substrate conditions are crucial in respect to sedimentation and deposition impacts. While substrate instability in former hard-bottom reefs causes species assemblages to change, those effects are minor in cases of similarities between the initial substrates and volcanic deposits (e.g., in areas with mud as primary substrate) (Heikoop, Tsujita, Heikoop, et al. 1996). Enhanced volcanic sedimentation rates and resultant dynamics in habitat

conditions (water and substrate) impose frequent perturbations which inhibit coral colonization, growth, and recovery to limit successional development of coral communities (Tomascik et al. 1997, 1996; Wilson and Lokier 2002). Consequently, affected reefs may disappear, as seen along the eastern coastline of Lombok, Indonesia, where fluvial transport of volcanic material into the coastal zone has continued since the Samalas eruption of 1257 (Mutaqin, 2020).

3.3.2. Turbidity and shading

Turbid water conditions resulting from direct material deposition, subsequent reworking of loose particulate matter, hydrothermal venting, submarine eruptions, or terrestrial runoff are commonly associated with volcanic activities (Table 3.1) (e.g., Bearden et al., 2005; Eldredge & Kropp, 1985; Reuter & Piller, 2011; Smallhorn-West et al., 2020; Vroom & Zgliczynski, 2011). As a consequence of high water turbidity, light exclusion significantly slows down photosynthetic activities. Furthermore, coral growth rates and reproduction are impaired (Storlazzi, Norris, and Rosenberger 2015). This can result in bleaching and mortality and therefore affects reef development (Rogers 1979; Wilson and Lokier 2002). Such perturbations can persist over prolonged periods of time following distinct eruption events (Barber et al. 2002; Houk 2011; Vroom and Zgliczynski 2011; Wilson and Lokier 2002). Specific implications are induced by the particular physical characteristics of (young) volcanic soils: dark coloured, fine particulate sediments are characterized by slow aquatic settling and high resuspension rates. Consequently, fine volcanic materials block light more efficiently than coarser or light-coloured carbonate sediments with respective impacts on reef health and productivity (Schleyer et al., 2016; Storlazzi et al., 2015; Takesue & Storlazzi, 2019; Wilson & Lokier, 2002). Thinning of the photic zone leads to changes in niche profiles over the depth gradient at reef scale, which alters species composition in regard to the exclusion of species intolerant to turbid conditions (Wilson and Lokier 2002). Turbid water conditions are often coupled with ongoing material sedimentation (Bearden et al. 2005; Wilson and Lokier 2002).

3.3.3. Nutrient addition

Essential nutrients for biotic productivity, such as iron, phosphate, nitrate, and silica are present in tephra (e.g., Flaathen & Gislason, 2007) and other volcanic products. In marine waters locations where these ions are biologically-limiting, their release can stimulate growth of autotrophic marine plankton organisms, collectively known as phytoplankton (Achterberg

et al. 2013; Browning et al. 2015; Duggen et al. 2007; Frogner, Gíslason, and Óskarsson 2001; Olgun et al. 2011). Returning nutrients to the light-influenced photic water zone at the sea surface by upwelling and overturning of thermal water column stratification may alternatively be caused by volcanically-induced sea surface cooling (Genin et al. 1995), or sub-surface water warming from lava inflow (Wilson et al., 2019).

While there is no published record of increased post-eruption chlorophyll concentrations impacting coral reefs, analysis of satellite data from Anatahan following the eruption in 2003 revealed elevated planktonic productivity for several weeks. Daily mean values of chlorophyll a concentrations in a 500 km buffer zone around Anatahan over the annual cycle were derived from MODIS Aqua satellite imagery. The data showed an anomalous peak in July 2003 around three months after the start of the volcanic activities on 10th of May 2003 in comparison to the chlorophyll concentrations in years without volcanic activities (Fig. 3.2). Those findings indicate a time-lagged biotic productivity response following volcanic activities with tephra fallout into the ocean. The observed pattern illustrates the effects volcanic nutrient influx can cause in marine waters. While effects on the coral reefs resulting from the additional nutrient influx, like reported from the Red Sea (Genin et al. 1995) and from Pagan in the Mariana Islands (Schils 2012), no such survey was carried out during the period of climax chlorophyll concentration after Anatahan's eruption in 2003. When the ecological state of the coastal reefs was monitored on 24th of August 2003 (Vroom and Zgliczynski 2011) no signs of impacts on the coral reefs resulting from volcanically-induced water fertilization were noted.

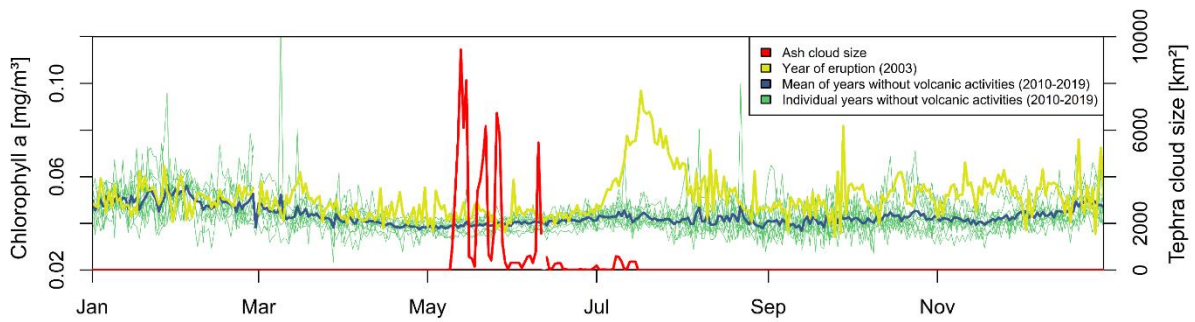


Figure 3.2: Daily mean chlorophyll *a* concentration in a 500 km buffer zone around Anatahan over the annual cycle derived from MODIS Aqua satellite data (NASA Goddard Space Flight Center, Ocean Biology Processing Group 2014). The year of the eruption (2003) is shown by the yellow line enabling comparisons with ten years without any reported volcanic activities (2010-2019) which are displayed by the blue line representing the mean of all years and the multiple green lines showing all years individually. The size of the emission cloud is represented by the red line. The data of the volcanic plume size was extracted from Volcanic Ash Advisory reports filed by the Darwin Volcanic Ash Advisory Centre (Darwin VAAC 2020).

Irrespective of the specific process involved, excessive nutrient addition to the photic zone may trigger cascadic ecological and biogeochemical effects including changes to coral reefs, such as a decline of coral cover and proliferation of macroalgae or cyanobacteria (Fabricius 2005; Schils 2012). Observed peaks in primary productivity with chlorophyll increases up to five or even 17 times (Lin et al. 2011; Mantas, Pereira, and Morais 2011) during phytoplankton blooms might reach levels critical to coral survival (Abram et al. 2003; Bell, Elmetri, and Lapointe 2014). Associated threats to reef health include reduced light penetration and inhibition of water circulation by overgrowth of filamentous algae as well as oxygen depletion (Genin et al. 1995; Lokier et al. 2009; Wilson and Lokier 2002), and red tides causing reef mortality from asphyxiation (Abram et al. 2003). Those factors can be synergistic and induce detrimental impacts on coral reef organisms resulting in disease (Haapkylä et al., 2011) and nuisance species outbreaks (Schils 2012). Ultimately, coral reef mass mortality events from nutrient excess can result in reef degradation (Genin et al. 1995).

3.3.4. Other changes to seawater chemistry

Seawater salinity is affected by the connectivity of coastal zones to adjacent terrestrial aquifers. High porosity of volcanic bedrock can enhance direct freshwater input into nearshore waters, thus lowering marine water salinity levels with potential implications on coral health. In the Northern Mariana Islands, relative high salinity was found beneficial to coral growth, abundance and diversity, whereas lower salinity from porous bedrock promoted algal occurrence with low structural reef complexity (Houk 2011; Houk and Starmer 2010).

Ocean water acidification is a common consequence of tephra fallout (Duggen et al. 2010) resulting from strong mineral acids contained in tephra leachates (Stewart et al. 2006). CO₂ influx from submarine volcanic degassing seeps also alters seawater carbonate chemistry and lowers pH as the gas dissolves and reacts with water to form carbonic acid and dissociates. Variations in pH and dissolved inorganic carbon speciation are known to impact skeletal calcification and reef community shifts (Cattano et al. 2020; Enochs et al. 2015; Hall-Spencer et al. 2008) (Fig. 3.6 i). Nutrient enrichment and reduced oxygen concentrations were also documented around submarine vents (Januar et al. 2017; Santana-Casiano et al. 2013). Around 80% of current volcanic eruptions are estimated to occur in submarine settings (Siebert and Simkin 2002) and potentially induce significant localized impacts on coral reefs ecosystems. However, studies on shallow water coral communities exposed to hydrothermal volcanic venting show mixed results reflecting volcanic activity (e.g., Enochs et al., 2020; Januar et al., 2017; Oprandi et al., 2019). For example, corals were found resilient to periodic acidification from CO₂ seeps in nearshore reefs in St. Vincent and the Grenadines (Enochs et al. 2020), whereas increased water acidity from continuous hydrothermal venting at shallow-water sites in Indonesia was found to be less influential in shaping coral community structures in comparison to associated nutrient input (Januar et al. 2017). Community responses commonly favour massive corals which are more tolerant of lower seawater pH (O'Brien et al. 2018), whereas branching corals are significantly impaired (Strahl et al. 2016). In addition to chemical alterations, submarine volcanoes cause thermal anomalies, sedimentation, and water turbidity (Mantas et al. 2011; Smallhorn-West et al. 2020).

In terms of chemical water alterations, volcanically-induced concentration increases of aluminium and copper (Duggen et al. 2007), mercury (Huang et al. 2018), hydrogen sulphide (Richoz et al. 2012), manganese (Shen et al. 1991), and anomalous rare earth element enrichment greater than the factor of three were linked to coral impacts (Wu et al. 2018). Observed consequences of elevated concentrations of those substances include coral species loss, mass mortality, and cessation of reef growth (Huang et al. 2018; Richoz et al. 2012; Wu et al. 2018).

3.3.5. Tsunami

Triggered by various volcanic mechanisms including cone collapse, flank failure, landslides, or pyroclastic material flow into the sea, extreme explosive eruptions can trigger tsunamis that affect distal coastlines thousands of kilometres away causing perturbations to local

benthic communities (Carey et al. 2001; Paris et al. 2014) (Fig. 3.6 g). Along shorelines in the Sunda Strait, deposits of a volcanically-induced tsunami from Krakatau in 1883, tens of kilometres away, contained biogenic carbonate fragments including parts of corals and other benthic organisms (van den Bergh et al. 2003; Carey et al. 1996, 2001; Paris et al. 2014; Putra and Yulianto 2017). Under the extreme wave movement, corals were damaged, dislocated, and washed up the shore (Carey et al. 2001; Simkin and Fiske 1983).

3.3.6. Temperature anomalies

Direct mortality and stress symptoms of sessile reef organisms and fish have been observed following seawater heating associated with submarine eruptions and lava flow into coastal reef zones (Dana 1872; Heikoop, Tsujita, Heikoop, et al. 1996; Heikoop, Tsujita, Risk, et al. 1996; Smallhorn-West et al. 2020; Tomascik et al. 1996). The degree of temperature change is determined by the mass influx rate (Grigg and Maragos 1974). Warming of about 3-20°C within just a few centimetres to hundreds of metres, was reported from lava influx in Hawaii and a hydro-magmatic eruption at Hunga Tonga–Hunga Ha’apai Island (Mantas et al. 2011; Moore et al. 1973; Smallhorn-West et al. 2020), whereas thermoremanent magnetization analysis of submarine facies indicated pyroclastic density currents impacted the substrate at temperatures > 450°C during Krakatau’s activities in 1883 (Mandeville et al. 1994). Due to the low density of heated water, discrete layers of buoyant water typically form at the surface (Moore et al. 1973). Such stratification within the water column results in highest impacts on coral in shallow waters with decreasing severity with water depth (Tomascik et al. 1997).

On a global level volcanic forcing is an important driver in the natural climate system (e.g., Crowley, 2000). During explosive eruptions, emitted tephra particles and photoactive aerosols, like sulphate dioxide, absorbs and backscatters solar irradiance (Fig. 3.1 d). This results in large-scale surface temperature cooling with complex implication to the global energy budget (IPCC 2021; Robock 2000). Such anomalies become effective at reef scale with a time lag of several months (Genin et al. 1995) and can last for years (Gagan et al. 2015; Kuhnert et al. 2000; Peñaflor et al. 2009). Volcanically-induced climate cooling can reduce coral growth (Felis et al. 1998). However, climatic implications from the large eruptions of El Chichón in 1982 and Mount Pinatubo in 1991 counteracted coral bleaching in the Caribbean. The spatial extent of coral die-off in the years after these eruptions was five times below bleaching levels during years without volcanic stratospheric aerosol loads (Gill et al. 2006).

In contrast to water heating from lava inflow, climatic cooling can cause destabilization of thermal stratification within the water column. Such thermal anomalies at the surface can result in decreased temperatures at reef scale as a consequence of deep water upwelling (Genin et al., 1995; Wilson et al., 2019). In the Gulf of Aqaba, northern Red Sea, temperature anomalies from atmospheric cooling induced by the eruption of Mount Pinatubo in 1991 weakened the thermal ocean water stratification. This triggered upwelling of nutrient rich deep water to cause a phytoplankton bloom at the surface. A cascading resultant effect was extensive overgrowth of corals by filamentous algae which resulted in mortality of many individual colonies (Genin et al. 1995).

3.3.7. Habitat formation

More than a century ago Charles R. Darwin and James D. Dana (Dana 1872; Darwin 1842) described the importance of volcanic activity for coral reef development around oceanic islands. According to Darwin's hypothesis of island genesis, volcanic islands form when submarine vents peak over the ocean surface. At a later state, islands converge to atolls when the volcanic edifice subsides and coral reefs grow in suitable shallow-water zones (Darwin 1842). Following up upon this model, Dana developed an advanced concept accounting for dynamics in island geomorphology over time (Johnson et al. 2018). Stable substrates of volcanic origin form suitable bases for coral settlement (Grigg and Maragos 1974; Jouval et al. 2020; Tomascik et al. 1996) and it has been reported that maximum carbonate accumulation occurs during and after periods of active edifice formation (Dana 1872; Takayanagi et al. 2012) in times of reduced volcanic activities (Huang et al. 2018; Königshof et al. 2010; Wilson and Lokier 2002). During those times, coral growth and reef development is promoted as ongoing marine erosion forms extensive shelf zones where fringing barrier reefs arise. With ongoing erosion of volcanic deposits and the edifice itself, terrestrial sediment influx decreases, thus minimising its limiting effects on reef expansion. Resultant larger reef zones generally host higher biodiversity, which in turn increases community resilience and promotes biogenic productivity of reef-associated calcifying organisms. At this point, insular persistence is attributed primarily to biogenic sedimentation (Ramalho et al. 2013). As a consequence of subsidence, reef platforms result from vertical reef accretion (Moore et al. 1990). Those guyots are exposed to ongoing marine erosion (Palmiotto, Corda, and Bonatti 2017; Terry and Goff 2013) and eventually reefs "drown" (Jones 1995).

Volcano-tectonic processes of coral reef habitat generation were found being stronger determinators of past reef formation than climatic controls of coral growth (Takayanagi et al. 2012). The importance of volcanic islands as “stepping stones” enabling long-distance larval dispersal and increasing connectivity of spawning coral populations around the globe is another aspect to the relevance of volcanism for reef habitat formation (Wood et al. 2014). In phases of extreme sea level fluctuations, steep volcanic slopes serve as refuge zones for corals by providing suitable habitat when sea levels change (Tomascik et al. 1997).

Apart from volcanic habitat creation, uplift of well-developed reef terraces above sea level will abruptly terminate benthic life. Such incidents were documented in Vanuatu and Rabaul Harbour (Chen et al. 1995; Yao et al. 2013).

3.4. Conclusion

The effects of volcanic activities can cause direct and indirect impacts on coral reefs. Direct impacts are typically associated with volcanic material deposition. The main driving hazard types are tephra fallout, lava flow, and pyroclastic currents (Grigg and Maragos 1974; Maniwavie et al. 2001; Smallhorn-West et al. 2020; Tomascik et al. 1996; Vroom and Zgliczynski 2011). Effects on coral reef organisms include physical destruction and smothering at high magnitude impacts. Under lighter exposition, corals show stress symptoms (Heikoop, Tsujita, Risk, et al. 1996). Physical damage can also result from floating pumice to cause scouring and removal of sessile benthic organisms (Eldredge and Kropp 1985). Another form of direct impacts is uplift or subsidence of reef terraces. In those instances reefs can be lifted out of the water (Chen et al. 1995) or reefs may drown (Jones 1995) with fatal consequences to coral reef organisms.

Indirect volcanic impacts affecting coral reefs primarily result from changes to habitat conditions. Substrate stability is a critical factor as stony corals require stable benthic surfaces for settlement (Maniwavie et al. 2001). Sedimentation of unconsolidated volcanic deposits induced by pyroclastic material influx typically forms loose substrates which hinder corals to grow (Reuter and Piller 2011; Smallhorn-West et al. 2020). Volcanic activities can also change ocean water quality at reef scale in terms of particle dissolution and chemical alterations (Tomascik et al. 1996). Turbid water conditions may result in reduced growth and limited productivity (Atrigenio et al. 1991; Reuter and Piller 2011; Vroom and Zgliczynski 2011). Nuisance species can spread when limiting key nutrients are introduced by

volcaniclastic influx (Schils 2012). Another factor is coral die-off from extreme water heating associated with lava flow into coastal coral reef zones (Moore et al. 1973). While such thermal implications are spatially limited, effects of volcanically-triggered atmospheric cooling may result in reduced coral growth rates over continental scales (Felis et al. 1998).

Apart from the various destructive effects of volcanic impacts on coral reef ecosystems, volcanic activities are ultimately a major driver of habitat formation for shallow-water reef organisms (Dana 1872; Darwin 1842; Piller and Riegl 2003; Tomascik et al. 1996). This duality reflects the complexity volcano-coral-interrelations.

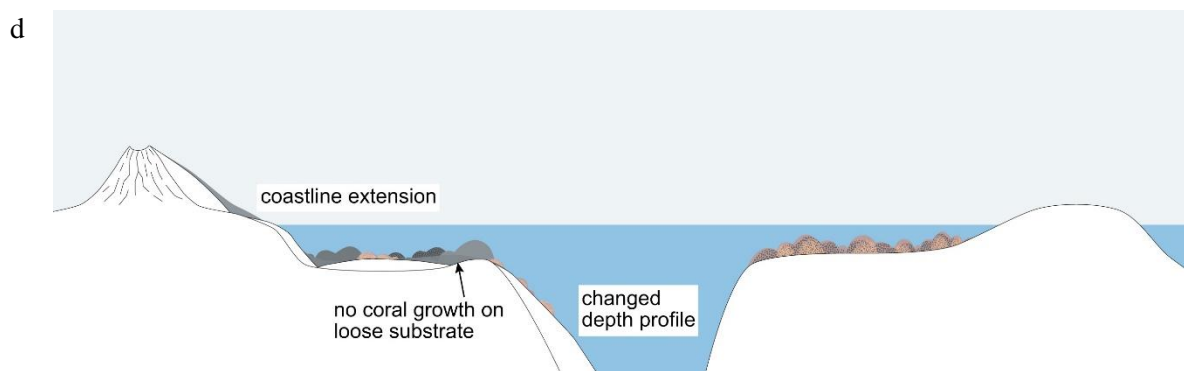
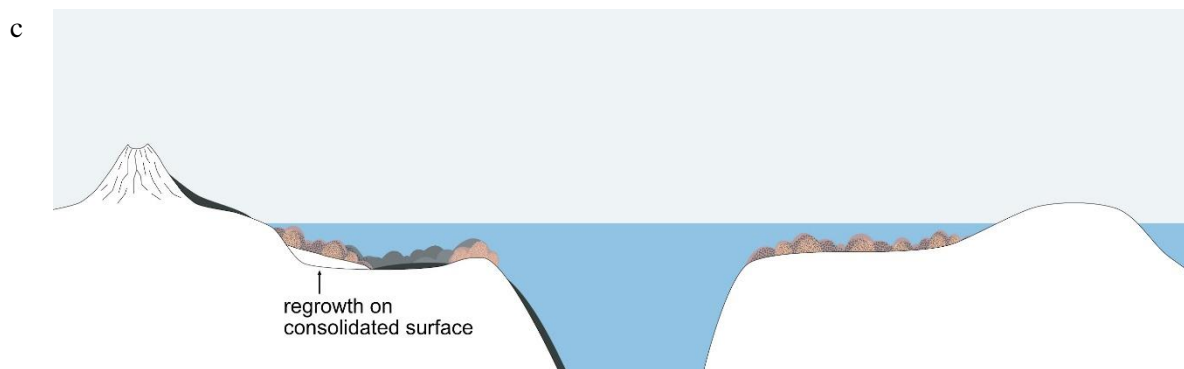
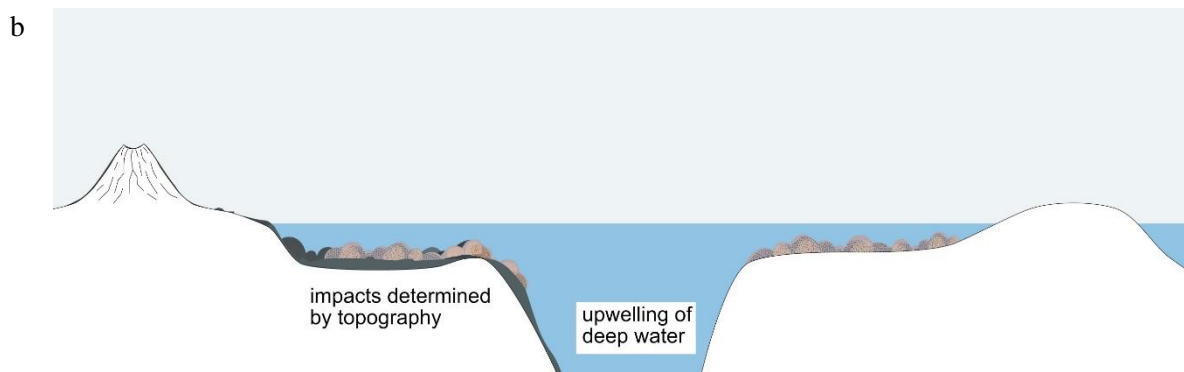
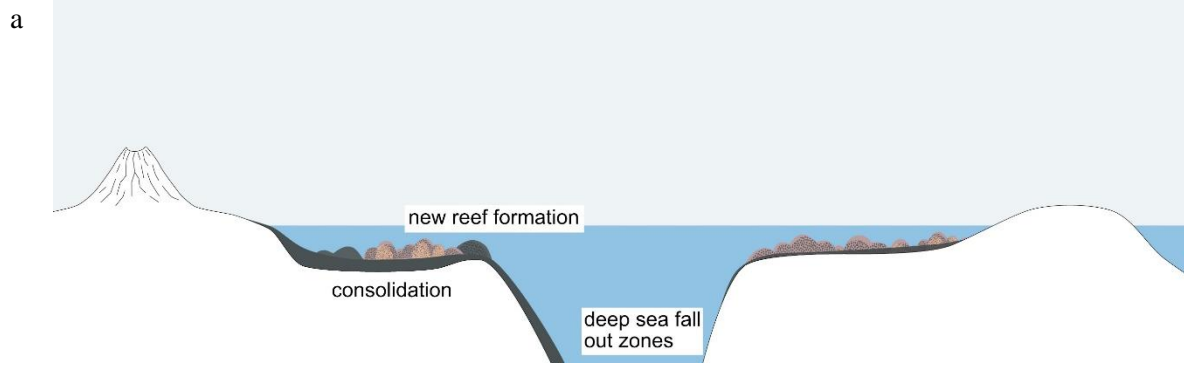
4. Chapter 4 – Patterns of coral reef recovery after volcanic perturbations

4.1. Introduction

Coral reef communities are abundant at volcanically affected locations around the globe (Groombridge et al. 2003; Spalding et al. 2001). In volcanic hotspot regions, like in the Coral Triangle in southeast Asia, a significant proportion of over 30% of coral reefs is located within 500 km of more than ten active volcanoes. Globally, over 60% of coral reefs lie within such distance from at least one active volcano (Fig. 1.2). Impacted coral reef organisms and communities typically recover after volcanic perturbations. For example, biogenic reef carbonate is found interbedded in volcanic deposits (Montaggioni and Martin-Garin 2020) and corals grow on volcanoclastic materials (Piller and Riegl 2003; Sluiter 1890). In this chapter time needed for coral reef recovery, implications from changed habitat conditions, and successional development of entire reef communities in the aftermath of volcanic disturbances are reviewed.

4.2. Habitat conditions determine coral reef recovery

Recovery of coral reefs from particular volcanic hazards reveals overall similarities in terms of the essential role of stable benthic substrates for coral growth. While no corals develop in areas of deep tephra deposition, stable benthic structures allow for settlement with new reef formation on consolidated and stable benthic surfaces (Fig. 4.1 a) (Maniwavie et al. 2001; Vroom and Zgliczynski 2011). Unlike submarine tephra deposits, lava flows provide such stable bases on which corals regrow in the case of sufficient larvae resources in the vicinity (Fig. 4.1 b) (Grigg and Maragos 1974; Tomascik et al. 1996). Same applies for pyroclastic deposits and erosive volcanic products: regrowth occurs on consolidated surfaces but ongoing deposition and limited substrate stability hinder the formation of well-developed coral reefs (Fig. 4.1 c and Fig. 4.1 d) (Piller and Riegl 2003; Sluiter 1890; Umbgrove 1930). In the case of volcanically-induced flank failure and associated tsunami generation, coral fragments that are relocated and washed up onto the shore (Carey et al. 2001; Paris et al. 2014) are unable to recover, while physically damaged colonies which remained partially intact may recover rapidly (Fig. 4.1 e) (Eldredge 1982). Observations indicate that hydromagmatic products form suitable substrates for coral settlement. Such reef formation in turn is suppressed by ongoing material sedimentation of young volcanic deposits (Fig. 4.1 f) (Smallhorn-West et al. 2020).



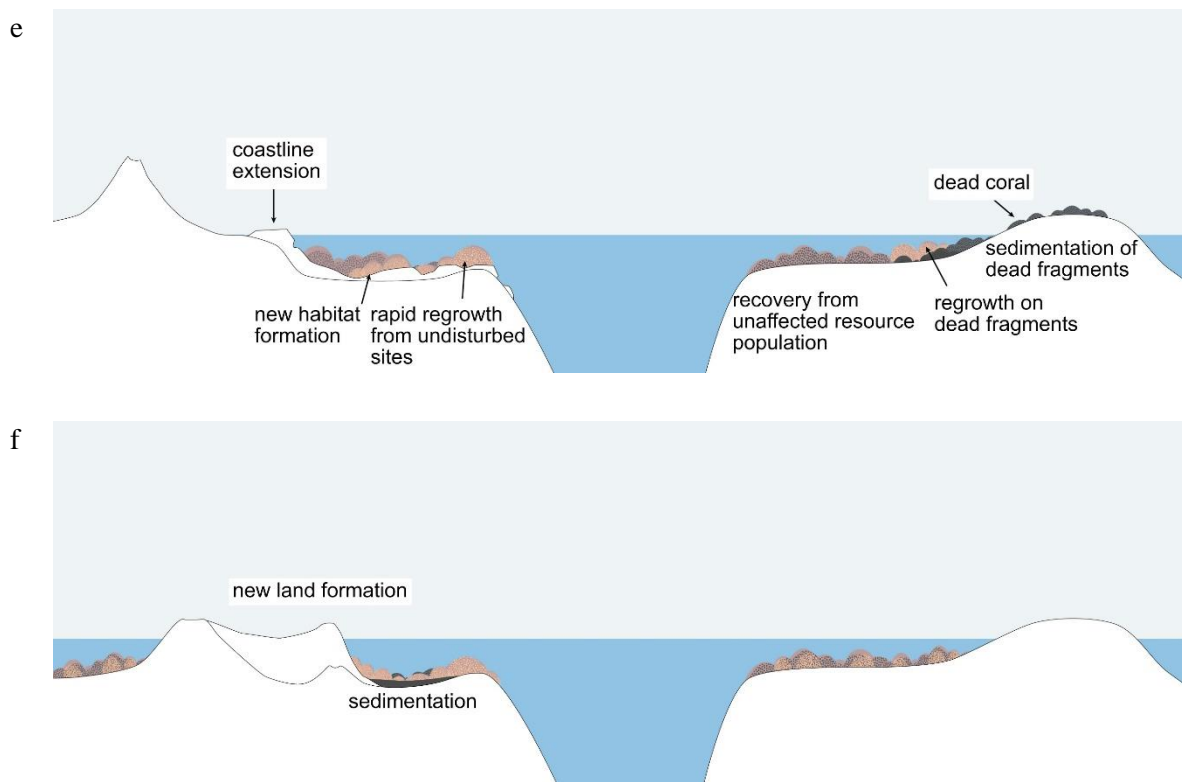


Figure 4.1: Coral reef recovery from volcanic impacts: a) tephra deposition, b) lava flow, c) pyroclastic density current, d) erosion of unconsolidated volcanic deposits, e) landslide and tsunami generation, f) Surtseyan eruption. Illustrations created by Nguyen Thi Nam Phuong, Earth Observatory of Singapore.

Changes in local habitat conditions critically impact coral reef recovery rates after volcanic perturbations. Corals cannot grow on unstable volcanic substrates formed by pyroclastic deposits (Eldredge and Kropp 1985; Houk and Starmer 2010; Maniwavie et al. 2001). Such foundations prevent settlement and therefore inhibit coral reef recovery (Grigg and Maragos 1974; Heikoop, Tsujita, Heikoop, et al. 1996). In areas of deep tephra fallout in Rabaul Harbour, large boulders, wooden debris, and dislocated coral fragments served as bases for reef formation (Maniwavie et al. 2001). However, rapid recolonization was observed once particulate matter from tephra deposition was cleared off coastal reefs by strong wave influence at Anatahan (Vroom and Zgliczynski 2011). Similarly, accelerated recovery in wave-affected zones is reported from multiple incidents of volcanic impacts including loose material deposition (Eldredge and Kropp 1985; Grigg and Maragos 1974; Heikoop, Tsujita, Heikoop, et al. 1996). Wave-induced resuspension, associated erosion, and sediment redistribution were instead found counteracting rapid benthic community reestablishment (Houk and Starmer 2010; Tomascik et al. 1996). The essential role of substrate stability for coral reef recovery can be illustrated by comparing the effects of the extreme eruptions of Samalás in 1257 and Tambora in 1815. Both stratovolcanoes are located in the Sunda Arc. Their large

eruptions (VEI 7) caused multiple hazards including tephra emissions and pyroclastic material surges into surrounding coastal waters (Kandlbauer and Sparks 2014; Vidal et al. 2015). Biodiverse and complex coral reefs with large individual specimens indicating no signs of adverse long-term effects were found in Sanggar Bay nearby Tambora (Best et al. 1989). Contrastingly, no fringing nearshore coral reefs exist over more than ten kilometres off terrestrial deposition zones along Lombok's coast over 750 years after Samalas' cataclysmic eruption. Riverine remobilization of volcanoclastic deposits adversely changed the local bathymetry, substrate, and water conditions to ultimately inhibit reef formation (Mutaqin 2020).

Lava flows, in contrast, form stable and structurally complex foundations free of predators and potential competitors that are suitable for coral settlement (Tomascik et al. 1996). Rapid recovery of species rich benthic communities within four years after a hydromagmatic eruption occurred in Hunga Tonga (Smallhorn-West et al. 2020) and a diverse coral community with 124 recorded species in total and live coral cover rates over 60% developed within five years on a submarine lava flow in Banda Api (Tomascik et al. 1996). However, recovery of coral communities on lava flows from Kīlauea took 20-50 years (Grigg and Maragos 1974) and in Reunion Island, coral diversity, density, and cover increased with flow age from ten up to 40 years (Jouval et al. 2020). In those instances other habitat characteristics, such as exposition to wave impacts and differences in climax community state are potential factors of lagged reef recovery (Grigg and Maragos 1974).

Ocean water conditions change more rapidly than reef substrates, therefore enabling fast reversal once phytoplanktonic and bacterial conditions have normalized after volcanic activities (Genin et al. 1995; Schils 2012). A quick return to pre-eruption conditions with hard coral prevalence coincided with the termination of Mount Pagan's light but ongoing volcanic activities from 2007 until 2011 (Schils 2012). Similarly, reef degradation in the northern Red Sea associated with changes in water temperature, chlorophyll, and nutrient concentrations was temporary and did not persist once those conditions changed back to pre-disturbance state (Genin et al. 1995). Stable overall habitat conditions without additional natural and anthropogenic stressors support quick ecosystem restoration once volcanic activities have ceased (Schils 2012; Smallhorn-West et al. 2020).

In contrast, increasing anthropogenic disturbance impacts reduce coral reef biodiversity and ecosystem functioning with potential negative impacts on natural recovery abilities

(Knowlton and Jackson 2008). Furthermore, chronic stress from water pollution and warming but also acute disturbance events can reduce recovery capacities of coral reefs (Ortiz et al. 2018; Osborne et al. 2017). Such cumulative disturbance impacts, e.g. from water quality deterioration and climatic changes, can exacerbate each other resulting in mutual negative influences to coral reef communities (Devlin et al. 2012). In terms of volcanic impacts, abrupt mortality to corals under thermal pressure was associated with light tephra deposition in the South China Sea (Wu et al. 2018). This indicates that coral reefs already affected by chronic stress exposure e.g. from warming ocean water are particularly sensitive to punctual volcanic events. Considering the effects of anthropogenic changes to natural coral reef disturbance regimes (Hughes et al. 2003; Nyström, Folke, and Moberg 2000) and predictions of climate change effects to reef ecosystems (Hoegh-Guldberg et al. 2007) points out a critical role of volcanic impacts to coral reef resilience. Exacerbating effects of cumulative pressure from interfering disturbances including volcanism might increase in the future. However, conservation measures integrated into local management strategies could help to promote recovery of impacted coral reefs (Devlin 2022).

4.3. Coral reef recovery times

Documented recovery times of coral reef communities significantly differ between case studies, reflecting impact type, severity, and persistence of habitat alterations induced by the disturbance but also initial state of the affected coral reef in terms of cover and species diversity. Looking at the shortest recovery times, rapid reversal within days to months is reported for reef rehabilitation from trophic changes and associated overgrowth by algae and cyanobacteria at Pagan Island (Schils 2012) and in the northern Red Sea (Genin et al. 1995). Discontinuities in coral growth associated with tephra deposition appear to last several months in massive *Porites* sp. colonies (Quinn et al. 2006). Recovery of physically impacted corals within months to years can occur via regrowth of extant colonies. This was reported for corals affected by various volcanic hazards, such as tephra fallout in Rabaul (Maniwavie et al. 2001), basal lava coverage in Hawaii (Moore et al. 1973), and pyroclastic material influx at Krakatau (Sluiter 1890). Evidence of regeneration on necrotic or covered tissue is seen in anomalous growth forms including deformed parts, dead-regrowth surfaces, stress bands, and skeletal material inclusion such as distinctive iron-rich “black bands” (Heikoop, Tsujita, Heikoop, et al. 1996; Heikoop, Tsujita, Risk, et al. 1996; Smallhorn-West et al. 2020; Wu et al. 2018; Yamashiro and Fukami 2012). Following the spectrum of reported times for

recovery, coral establishment on submarine lava flows forming communities with high diversity, abundance, and cover within 4-5 years were observed in Hunga Tonga and Banda Api (Smallhorn-West et al. 2020; Tomascik et al. 1996). More extensive time spans of 20-50 years were noted for community development on lava flows in Hawaii to match up with adjacent but unimpacted coral assemblages (Grigg and Maragos 1974). Similarly, altered species composition persisting over decades was detected for benthic assemblages along Reunion Islands volcanically affected eastern coast (Bollard et al. 2012; Jouval et al. 2020). Harsh environmental conditions characterized by occasional tephra fallout, ongoing erosion, sedimentation, resuspension, and deposition of volcanic materials were linked with coral reef recovery rates of around 90 years in the Northern Mariana Islands (Houk and Starmer 2010). Reconstruction of reefal carbonate production based on ^{14}C age dating indicated resumption after episodic tephra fallout within a century at the Huon Peninsula in Papua New Guinea (Pandolfi et al. 2006). Slightly longer of a recovery period for genetic rehabilitation of certain reef organisms occurring over ~120 years after benthic sterilization is reported from Krakatau (Barber et al. 2002; Starger et al. 2010). In most extreme cases, reef formation may be prevented for centuries under conditions of ongoing volcanoclastic sedimentation to permanently change coastal geology, substrate conditions, and water quality (Mutaqin 2020). An example is the lack of reef formations offshore fluvial runoff areas from deposits of Samalas' eruption in 1257 along the eastern coastline of Lombok in Indonesia (Mutaqin 2020). If reef terraces are lifted above sea level, biogenic carbonate production will cease completely (Chen et al. 1995).

Such great variation in coral reef rehabilitation rates mirrors the complexity of volcano-coral-coherence. Different volcanic hazards result in variant post-eruption habitat conditions, which determine recovery speed (Grigg and Maragos 1974; Houk and Starmer 2010). In addition, biogeographical aspects, like surrounding refugia for new recruitment and high population connectivity, are essential for reefs to rebuild (Barber et al. 2002; Smallhorn-West et al. 2020; Starger et al. 2010; Tomascik et al. 1996). Observations of coherence between maximum recruitment on lava flows and highest abundance in the vicinity indicate the importance of recolonization from local or regional source populations (Bollard et al. 2012; Grigg and Maragos 1974; Smallhorn-West et al. 2020; Starger et al. 2010; Tomascik et al. 1996). In essence, a healthy coral reef ecosystem will recover faster. Thus, a clear characterization of ecosystem succession dynamics requires consideration of eruption parameters, site-specific environmental and ecological conditions, as well as the initial state

of the impacted reef assemblage (Maniwavie et al. 2001; Smallhorn-West et al. 2020; Tomascik et al. 1996).

4.4. Successional trajectories of coral reef recovery after volcanic perturbations

In the absence of any disturbance to a natural system, competition for resources will form a climax community dominated by few species that are best adapted to the prevalent environmental conditions (Connell 1978; Whittaker 1974). Community development over the course of coral reef recovery is characterized by a successional sequence towards such climax community state (Pearson 1981) resulting in rebound to an ecological state comparable with pre-disturbance conditions (Pulsford, Lindenmayer, and Driscoll 2016). However, maximum species diversity is typically found at intermediate disturbance recurrence and magnitude. Accordingly, highest diversity within an ecosystem is maintained by ongoing changes in species composition as a result of frequent perturbations to interrupt competition and prevent an equilibrium stable state of communities (Connell 1978). This concept to describe the formation of biodiverse ecosystems, also known as the intermediate disturbance hypothesis (IDH) (Connell 1978), was applied to coral reefs in several instances (Aronson and Precht 1995; Connell 1978; Rogers 1993) including recovery of coral communities affected by volcanic disturbance (Grigg and Maragos 1974).

The observed successional trajectory of coral reef communities following lava influx conform this pattern (Grigg and Maragos 1974; Jouval et al. 2020). Coral reef community development is locally set back, delayed, or temporally prevented by direct eruption impacts or persistent habitat change from indirect volcanic impacts (Houk and Starmer 2010; Tomascik et al. 1996). Increasing species numbers following periods of active volcanism indicate stages of early succession. Such trends were observed among different functional groups of reef organisms including coral, reef fish, and echinoderms in Reunion Island (Bollard et al. 2012). After reaching peak levels, a decrease in species diversity developing towards original community composition was observed in coral resettlement on submarine lava flows in Hawaii and Reunion Island (Grigg and Maragos 1974; Jouval et al. 2020). The elevated coral diversity reported from a submarine lava flow in Banda Api in comparison to unaffected adjacent reef sites five years after the eruption (Tomascik et al. 1996) might represent a short-term peak in biodiversity prior to species losses due to the onset of intra- and interspecific competition for resources, which is reported to shape coral reef community composition in Hawaii and at Krakatau (Grigg and Maragos 1974; Putra et al. 2014).

Consideration of various case studies allows for deduction of a general successional trajectory of coral reefs following volcanic perturbations, which is illustrated in Fig. 4.4. Coral reef recovery from volcanic impacts depends on the exceedance of critical thresholds of habitat alterations. The initial volcanic impact may result in immediate and rapid decline in terms of species abundance, cover, and diversity throughout multiple functional groups in impact zones (Reuter and Piller 2011; Tomascik et al. 1996; Vroom and Zgliczynski 2011). Reef organisms are affected by burial, dislocation, physical destruction, and water quality deterioration (Pajaro et al. 1992). Destruction of benthic organisms may continue beyond the impact duration after volcanic activities ended (Eldredge and Kropp 1985; Houk and Starmer 2010; Reuter and Piller 2011). Regrowth from partially destroyed colonies and increasing suitable solid surfaces for settlement initiate coral reef recovery (Houk and Starmer 2010; Maniwavie et al. 2001; Vroom and Zgliczynski 2011). Further normalisation of habitat conditions enables settlement of generalist pioneer species (Bollard et al. 2012). Mostly juvenile specimens and the return of mobile organisms are noted over the course of recovery (Smallhorn-West et al. 2020). Subsequently, an ecological reef state comparable with pre-eruption conditions is reached. Overall species diversity, promoted by the formation of new and structurally complex habitat free of competitors and predators in the vicinity of abundant local and distant resource refugia, may further rise (Tomascik et al. 1996). As a consequence, a peak exceeding the local species richness of unaffected neighbour sites may emerge at intermediate disturbance magnitude and frequency (Grigg and Maragos 1974; Jouval et al. 2020; Tomascik et al. 1996). With the onset of inter- and intraspecific competition, resource monopolization induces shifts in community composition towards dominance of few specialists that are best adapted to prevalent habitat conditions (Grigg and Maragos 1974; Putra et al. 2014). Volcanic impacts without significant effects in terms of habitat alteration may result in selective declines among reef biota. Species that are able to escape from impact zones, reject superficial deposition, adjust feeding strategies, are of large morphological sizes, or occur in great abundance have higher chances to persist (Anthony and Fabricius 2000; Mendoza et al. 2020; Vroom and Zgliczynski 2011). Most abundant species in surrounding zones show maximum recruitment rates in disturbed areas (Tomascik et al. 1996) to allow for relatively quick return to pre-disturbance reef state once habitat conditions have normalised (Genin et al. 1995; Schils 2012). Similar to recovery from non-volcanic disturbances, speed of successional coral reef recovery from volcanic impacts is dependent on local circumstances in terms of community and functional resilience, abiotic habitat conditions, ecological factors, and disturbance intensity (Gouezo et al. 2019; Pearson 1981).

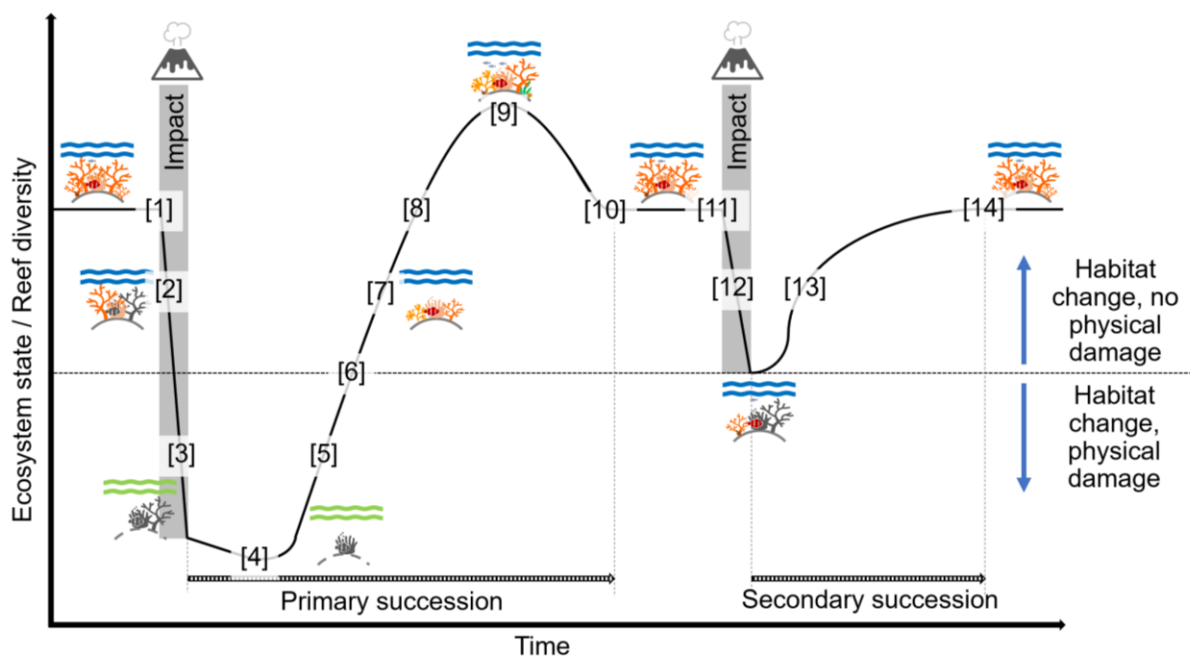


Figure 4.2: General pattern of successional coral reef recovery after volcanic perturbations: Following the initial impact [1] coral reef species abundance, cover, and diversity declines [2]. Individual organisms are affected by smothering, removal, and destruction associated with deterioration of habitat conditions [3] causing biotic damage even when volcanic activities have ceased [4]. With starting normalisation of habitat conditions and growth from persistent colony remnants, reef ecosystem recovery starts [5] enabling settlement of pioneers [6], growth of juvenile specimens, and return of mobile species [7]. Throughout further recovery, a reef state similar to pre-eruption conditions develops [8]. Subsequently, overall biodiversity may be elevated [9] prior to individual species exclusion from resource monopolization of few dominant species [10]. When volcanic impacts do not critically change habitat conditions [11], reef organisms decline selectively according to individual tolerance levels [12]. Species of highest abundance in the vicinity provide larvae influx for new recruitment [13], which facilitates return to pre-disturbance reef state under normalised habitat conditions [14]. Note that the temporal dimension in this illustration is not linear. Substrate unsuitable for coral settlement is symbolised by dashed lines, reduced water quality is indicated by green waves, and dead reef organisms are displayed by grey symbols in this figure. The volcano icons represent volcanic pulse perturbations.

The outlined successional development is characterized by species turnover during which generalist pioneers are subsequently suppressed by more specialized species (Tomascik et al. 1997). A pattern also found in deep sea benthic foraminifera communities under the influence of tephra fallout from the Pinatubo eruption in 1991 (Hess et al. 2001). Time needed for recovery varies among different coral genera. As an example, on basaltic lava flows in Hawaii, *Pocillopora* sp. were pioneers, whereas other species, like *Montipora verrucosa*, were excluded from the site for at least a decade following the disturbance (Grigg and Maragos 1974). Just eleven out of 86 coral species that were found in Reunion Island occurred on lava flows. Here, 36 species in total were not found at any volcanically-affected site (Jouval et al. 2020). These community patterns show species-specific sensitivity to volcanic perturbations. Early successional domination by *Pocillopora* sp. was also recorded

on lava flows and in volcanic deposition zones in different regions (Grigg and Maragos 1974; Maniwavie et al. 2001; Putra et al. 2014; Tomascik et al. 1996). In terms of growth form, branching coral species, such as *Acropora* sp., were found settling first on stable lava flows, while encrusting colonies of *Montipora* sp., *Porites* sp., and branching *Pocillopora* sp. were found coping best with unstable pyroclastic substrates (Tomascik et al. 1996). Massive growth morphologies were not present in Krakatau in the first years after the 1883 eruption. Here, branching *Acropora* sp., *Porites* sp., *Favia* sp., and *Madrepora* sp. were found after five years following the volcanic destruction (Sluiter 1890). A sequence with initial growth of different morphology types including branching, tabular, massive, and encrusting corals followed by spread of *Acropora* sp. and superficial overgrowth by *Montipora* sp. to stabilize the substrate by encrusting rocks and cobbles was documented on lava flows from Mount Agung that reached the sea in 1963 (Piller and Riegl 2003). Along Bali's volcanically-affected north-eastern coastline, species composition changed over the course of reef development resulting in dense thicket formation on volcanic boulders. Apart from direct stabilization of the seabed, coral formations were found mitigating wave energy thus preventing submarine erosion (Piller and Riegl 2003).

Positive effects of volcanism contributing to coral reef health that result from reduced human pressure by intermitted tourism and fishing activities in evacuations zones during and after eruptions were observed in Bali (pers. comm. Derta Prabuning, Reef Check Indonesia). However, to best knowledge, this observation was not yet quantified nor scientifically discussed.

4.5. Conclusion and future perspective

Coral reef recovery from any disturbance is complex because it depends on many factors including impact characteristics, initial ecological status, species tolerance levels, and potential additional stressors (Graham et al. 2011; Pearson 1981). Considering the variety of volcanic activities, their variable severity, and rarity, it is not surprising that reported recovery times differ greatly from rapid reversal back to pre-disturbance reef state under light impacts (Schils 2012) up to inhibition of reef development over millennia (Mutaqin 2020). Those differences can be explained by changed habitat conditions resulting from volcanic activities. Presence of stable benthic surfaces suitable for coral settlement is especially critical from coral reef recovery (Maniwavie et al. 2001; Tomascik et al. 1996; Vroom and

Zgliczynski 2011) as changes to the substrates are associated with multiple volcanic hazards (Reuter and Piller 2011).

A common pattern of coral reef recovery from volcanic disturbances emerges from reports of multiple case studies (Fig. 4.4). A sharp decrease in coral reef diversity is associated with initial volcanic impacts (Reuter and Piller 2011; Vroom and Zgliczynski 2011). In case of persistent habitat changes, ongoing disturbance effects hinder reef reestablishment (Houk and Starmer 2010). Once habitat conditions have normalised, coral species resettle according to specific tolerance levels. For a limited period of time, the community is characterised by a plus in diversity (Tomascik et al. 1996) until the onset of competition for natural resources induces a return to pre-disturbance community state (Grigg and Maragos 1974). If colonies are just partially damaged by the eruption effects, full reef recovery is dominated by regrowth of extant remnants (Eldredge and Kropp 1985; Maniwavie et al. 2001).

However, alternating sediments of biogenic carbonate and volcanic materials (Montaggioni and Martin-Garin 2020; Wilson and Lokier 2002) and high contemporary abundance of diverse benthic assemblages at locations of ongoing volcanic upheaval (Groombridge et al. 2003; Spalding et al. 2001), demonstrate the abilities of reef communities to resettle and thrive despite or potentially even because of active volcanism. This conforms with the theories of island genesis and coral reef formation proposed by C. R. Darwin (1842) and J. W. Dana (1872) and furthermore reflects the predictions of the intermediate disturbance hypothesis (Connell 1978). Supporting evidence includes observations of coral settlement on submarine lava flows of different ages from 1.6 to 102 years in Hawaii (Grigg and Maragos 1974).

Volcanic activity provides valuable opportunities to study successional reef recovery as all benthic life can locally be removed by hazards such as e.g., lava flow (Tomascik et al. 1996). However, studies on successional recovery are limited (Grigg and Maragos 1974; Jouval et al. 2020). The resultant lack in empirical data might be attributed to the unpredictability and rarity of volcanic eruptions, the dangerous surrounding conditions during activities, and remote location of many active volcanoes (Vroom and Zgliczynski 2011). Consequently, evidence-based knowledge on recovery and succession of coral reef communities following volcanic perturbations is constrained (Smallhorn-West et al. 2020). The need for long term data of reef responses to volcanic hazards is expressed in the literature (Maniwavie et al. 2001). Therefore, this gap should be addressed as prerequisite of informed management

including implications from rare but potentially severe natural hazards to coral reef ecosystems.

5. Chapter 5 – Modelling tephra fall hazard to coral reefs in the Coral Triangle

Based on the previously outlined impacts volcanic activities can impose on coral reef ecosystems, this section forms a complement of application by simulating potential hazards from tephra deposition on coral reefs in southeast Asia. The aim is to locate regions of highest deposition loads and estimate average recurrence intervals at pre-defined threshold values of volcanic material deposition.

5.1. Introduction

The Coral Triangle (CT) in southeast Asia is the contemporary global centre of marine biodiversity (Hoeksema 2007; Renema et al. 2008; Roberts et al. 2002). This Indo-Pacific region is home to over 75% of scleractinian corals found on Earth (Hughes et al. 2013; Veron et al. 2009). More than 120 million people in the wider area rely on marine resources and ecosystem services for food security, sustained livelihoods, and economic wealth (Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security 2009; Foale et al. 2013; Hoegh-Guldberg et al. 2009). However, overexploitation, destructive fishing, coastal development, habitat alteration, pollution, and climate change affect over 90% of the regional coral reefs (Burke et al. 2012; Hoegh-Guldberg et al. 2009). Live coral cover decreased over the past decades (Souter et al. 2020) and one third of coral reefs in Indonesia is in poor ecological state (Hadi et al. 2020). Over geological timescales, the CT is also a tectonically active region particularly exposed to volcanism (Small and Naumann 2001), with more than 20% of all Holocene active volcanoes (Jenkins, Magill, et al. 2012; Siebert and Simkin 2002) (Fig. 5.1), which are prone to explosive volcanism because of their subduction zone setting (Siebert and Simkin 2002). This study addresses the ecological risk explosive volcanism poses to coral reefs in the CT by quantifying the likelihood and recurrence intervals of potential impacts from volcanic tephra deposition on coral reefs.

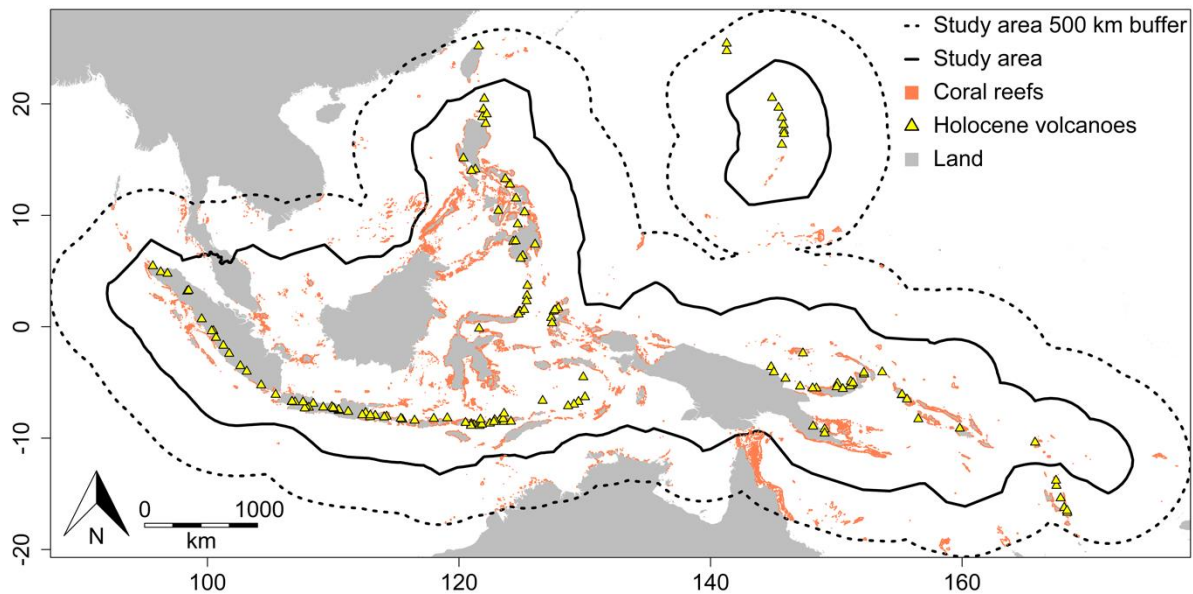


Figure 5.1: Coral reefs (UNEP-WCMC et al. 2010) and Holocene active volcanoes (Global Volcanism Program 2022) located in the study area as outlined by the implementation zone of the Coral Triangle Initiative on Coral Reefs, Fisheries, and Food Security (Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security 2009; Fidelman et al. 2012; Weeks et al. 2014). The area is complemented by the exclusive economic zones (EEZ) of the Northern Mariana Islands and Guam (Flanders Marine Institute 2019). The land mask was retrieved from Natural Earth (naturalearthdata.com).

Volcanism has shaped coral reef communities throughout their evolution (Arefifard and Payne 2020; Huang et al. 2018; Landwehrs et al. 2020; Shen et al. 2010; Wang et al. 2011). Volcanic hazards can temporarily eliminate marine benthic life and modify habitats at reef scale for centuries (Mutaqin 2020; Pandolfi et al. 2006; Tomascik et al. 1996). During explosive volcanic eruptions, magma is fragmented into particles, with airborne particles referred to as tephra and the smallest fraction of tephra (particle diameter < 2 mm) also referred to as volcanic ash. Tephra fallout is one of the farthest-reaching volcanic hazards affecting areas thousands of kilometres from the volcano, with particle size and ground accumulation typically decreasing with distance (Blong 1984; Jenkins et al. 2014; Sparks et al. 1997). As tephra comprises small blown-apart pieces of volcanic rock and glass, its texture is hard, abrasive, and it does not dissolve in water. Tephra can also have an acidic coating that leaches off upon contact with water. As a result, tephra fallout can cause environmental impacts, affect human health, induce socio-economic disruption, and physical damage (Ayrís and Delmelle 2012; Jenkins et al. 2014; Loughlin et al. 2015).

In coral reefs, tephra deposition can rapidly bury benthic communities (Maniwavie et al. 2001; Pandolfi et al. 2006; Tomascik et al. 1996; Vroom and Zgliczynski 2011), with individual colony damage and mortality resulting from smothering, breakage, and harm to tissue (Eldredge and Kropp 1985; Pandolfi et al. 2006; Reuter and Piller 2011). The health,

abundance, and diversity of different functional groups within coral reef communities can also be affected by changes to substrate stability, water chemistry, suspended particulate load, light availability, and nuisance species spread (Maniwavie et al. 2001; Reuter and Piller 2011; Schils 2012; Vroom and Zgliczynski 2011). Those impacts are detailed in the previous sections of this thesis.

Coral cover loss caused by tephra fallout has only been documented for a limited number of eruptions (Atrigenio et al. 1991; Maniwavie et al. 2001; Ochavillo et al. 1992; Ono et al. 2002; Pajaro et al. 1992; Vroom and Zgliczynski 2011). Here, this published evidence is collated to quantify the magnitude of tephra fallout associated with live coral cover change for the first time. A set of thresholds in terms of coral cover response and species sensitivity is characterised. Those critical values are referred to tephra dispersal rates and local levels of ground deposition simulated with the advection-diffusion model Tephra2 (Biass et al. 2016; Bonadonna 2005; Bonadonna et al. 2012) to assess regional hazards to coral reefs from tephra fallout in the CT. The chosen probabilistic modelling approach is based on stochastically sampling of possible input parameters from pre-defined ranges to simulate realistic and statistically significant eruption scenarios. The method was applied in comparable contexts (e.g., regional tephra fall hazard assessment to urban areas by Jenkins, McAneney, et al. 2012) and proved suitable for hazard quantification over continuous geographical scales. Therefore, spatial variations and local hotspots in volcanic risk exposure can be detected.

5.2. Material and methods

The method of tephra hazard assessment was adapted from Jenkins et al. (2012). The setting of adequate threshold values for estimation of impacts from tephra deposition on coral reefs was particularly addressed based on all available records setting tephra fallout rates in relation to coral cover changes.

5.2.1. Study region

The Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI) is a multilateral agreement aiming to preserve the marine and coastal resources in southeast Asia (Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security 2009; Fidelman et al. 2012; Green and Mous 2008; Weeks et al. 2014). Referring to this administrative domain, the CT is defined as the implementation zone of the CTI in this study. The presented volcanic

hazard assessment to coral reefs focuses on the implementation zone of the CTI outlined by the exclusive economic zones (EEZ) of its member states (Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security (CTI-CFF) 2009; Weeks et al. 2014) complemented by the EEZ of Singapore, the Commonwealth of the Northern Mariana Islands, and Guam (Fig. 5.1). Singapore, whilst not part of the CTI, is located inside the area and was therefore included. The Northern Mariana Islands and Guam were added because of past and recent scientific documentation of tephra impacts on coral reef communities (Eldredge 1982; Eldredge and Kropp 1985; Vroom and Zgliczynski 2011). All data used in this study is detailed in Tab. A1 in the appendix.

To identify volcanoes that may affect the CT, terrestrial Holocene active volcanoes with confirmed eruptions (Global Volcanism Program 2022) that had previously been assigned intensity-specific annual eruption probabilities (Loughlin et al. 2015) were considered. Only volcanoes located inside the study region or within a surrounding 500 km buffer were retained (Fig. 5.1), resulting in 137 volcanoes in total. The 500 km buffer was applied to account for any volcanic fallout impacts in the study area originating from adjacent volcanoes.

5.2.2. Coral reef responses to tephra fallout

Live coral cover is the most commonly-used measure in ecological coral reef assessment to monitor long-term changes and impacts of disturbance events (DeVantier and Turak 2017; Souter et al. 2020). A comprehensive literature search building up upon the review presented in previous chapters was undertaken to collate all available scientific literature quantitatively recording change in live coral cover in response to volcanic material fallout (Tab. 5.1). In original sources, the volcanic hazard was typically referred to as “ash fall” without any reference to size fractions provided. Therefore, it was assumed that tephra was meant.

To quantify live coral cover change as a consequence of tephra deposition, it is essential to compare volcanically affected reefs with direct tephra deposition with unimpacted sites. Environmental and ecological habitat conditions at the impacted and the reference sites should ideally be similar but differ exclusively in terms of the volcanic disturbance. The compiled records provide either spatial or temporal references. As coral cover naturally varies within and between sites in different regions in response to a wide range of local influence factors, temporal data provides the most robust response to a specific impact of

interest. Live coral cover assessments undertaken prior to and after tephra deposition events at the same location form such temporal references. As an example, benthic cover surveys were carried out at Capones Island before and after tephra fallout from Pinatubo's eruption in 1991 (Pajaro et al. 1992). Therefore, this data set provides pre- and post-eruption estimates on live coral cover at the same locations, which enable quantification of change rates in live coral cover attributed to tephra deposition. In this example, live coral cover of ~50% prior to the eruption was reduced to ~10% after tephra fallout (Pajaro et al. 1992). Where time series records on live coral cover development at impacted reefs were not available, live coral cover estimates from ecologically comparable but unaffected reference sites from different locations were used as best estimates serving as spatial references. Such records include benthic reef cover estimates from nearby sites without tephra deposition over a gradient of disturbance impacts such as the live coral cover estimates carried out around Anatahan and Sarigan in the Northern Mariana Islands following Anatahan's eruption in 2003. The range in live coral cover of the coastal coral reefs in the tephra fallout zone around Anatahan was 0-35% (SD 6.5%) under various levels of material deposition in comparison to 2.5-68.8% (SD 15.1%) around Sarigan, which is the closest neighbour island located ~40 km to the northeast and was not impacted by tephra fallout (Vroom and Zgliczynski 2011). Despite the inconsistency resulting from inclusion of spatial and temporal references, this approach was taken to make use of all available data.

Whether temporally- or spatially-referenced, relative percentage of live coral cover change from tephra impacts was calculated as a function of the median live coral cover of a site (i) for a specific isopach thickness relative to the reference coral cover value (ref) from a respective site without tephra deposition:

$$\% \text{ coral cover change}_i = \left(\frac{\% \text{ coral cover}_i - \% \text{ coral cover}_{ref}}{\% \text{ coral cover}_{ref}} \right) * 100 \quad (1)$$

A similar approach was chosen by Ochavillo et al. (1992) to calculate changes in fish biomass in areas of tephra deposition in comparison to the least impacted site.

Data accuracy of benthic cover estimates is barely documented (Hochberg and Gierach 2021; Vroom and Zgliczynski 2011). Therefore, standard errors of reported live coral cover rates were extracted from (Nadon and Stirling 2006). A relative value of 30% uncertainty for assessments via line transect was selected as most of the consulted studies use this method for visual coral cover sampling (Tab. 5.1). In one case of more detailed data on coral cover from

the Northern Mariana Islands (Vroom and Zgliczynski 2011), the relative standard error (rSEM) was calculated from the stated standard deviation from mean coral cover:

$$rSEM = \left(\frac{\frac{SD}{\sqrt{n}}}{coral\ cover_{mean}} \right) * 100 \quad (2)$$

SD is the standard deviation from mean coral cover, *n* is the total number of records, and *coral cover_{mean}* is the mean coral cover per site.

Quantification of tephra isopach depth in relation to changes in live coral cover were only presented in two of the consulted studies. For coral cover observations following the 1991 Pinatubo eruption, isopach lines and reported deposit depths were directly referred to live coral cover values (Atrigenio et al. 1991; Ochavillo et al. 1992). No such specification was available for the other studies. Therefore, regional isopach maps were used to estimate local tephra accumulation on the ground and at sea surface level at the specified reef survey locations. For Anatahan, the isopaches presented by Trusdell et al. (2005), for Rabaul, those by Blong (2003), and for the coastal zones of Zambales east of Pinatubo, those provided by Atrigenio, Aliño, and Biña (1991) were used. Isopachs provide contours of equal deposit thickness and following standard approaches the lower value was assigned to sampling sites located between isolines. As natural variance is inherent to any assessment of tephra isopach thickness, uncertainties of 9% for measured isopach depth and 30% for the average error resultant from natural variance in deposits were applied based on error quantification from reanalysis of tephra deposition by Engwell, Sparks, and Aspinall (2013).

Table 5.1: *Compiled records of coral reef responses under tephra deposition from seven studies on four different eruption events.*

Volcano, year of reef-impacting eruption	Location of coral reef sampling	Reference between impacted and non-impacted survey sites	Total number of records	Total number of isopach levels	Mean number (range) of records per isopach level	Hazard to coral reefs	Source of coral records	Method of reef assessment	Source of isopach depth	Method of isopach measurement
Anatahan, 2003	Anatahan and Sarigan, Northern Mariana Islands	Spatial gradient, different islands ~40 km apart	164	9	18.2 (3-54)	Tephra deposition, turbidity	Vroom and Zgliczynski 2011	Line transects, towed-diver surveys, photo-quadrats	Trusdell et al. 2005	Isopach maps derived from field thickness measurements at 49 sites on the island
Pinatubo, 1991	different coastal sites off Zambales, Philippines	Spatial gradient, deposition gradient along exposed coastline	5	4	1.25 (1-2)	Tephra deposition, lahar sedimentation, turbidity	Atrigenio, Aliño, and Biña 1991	Not specified	Atrigenio, Aliño, and Biña 1991	Isopach map
			4	2	2 (2-2)	Tephra deposition, lahar sedimentation	Ochavillo, Hernandez, and Aliño 1992	Line transects	Ochavillo, Hernandez, and Aliño 1992	Tephra deposits reported by the Philippine Institute of Volcanology and Seismology
		5	4	1.25 (1-2)	Tephra deposition	Pajaro et al. 1992	Line transects	Atrigenio, Aliño, and Biña 1991	Isopach map	
Tavurvur and Vulcan, 1994	Rabaul Harbour, Papua New Guinea	Temporal gradient, pre- and within 2 years post-eruption	2	2	1 (1-1)	Tephra deposition, drifting pumice	Maniwavie et al. 2001	Not specified	Blong 2003	Isopach map
Sakurajima, 1982	Kagoshima Bay, Japan	Temporal gradient, pre- and within 2 months post-eruption	2	2	1 (1-1)	Tephra deposition	Ono, Reimer, and Tsukahara 2002	Quadrat transects	Ono, Reimer, and Tsukahara 2002	Direct measurement (not specified)

5.2.3. Defining tephra thickness thresholds for coral cover change

Identification of critical thresholds of tephra deposition is an essential prerequisite for volcanic risk assessment (Biass and Bonadonna 2013). Such defined values provide an estimate of expected loads of tephra to cause specific damage. Hazardous deposit thresholds are typically informed by observational records of negative effects and field investigations following volcanic impacts (Blong 1984; Bonadonna 2005) and extracted from published literature (Biass and Bonadonna 2013; Michaud-Dubuy, Carazzo, and Kaminski 2021). Accordingly a conservative approach for critical threshold selection based on documented observational records was chosen. Thresholds were set where material fallout was found causing remarkable relative coral cover changes that can intuitively be understood and quantified, e.g., 100% live coral cover loss at a particular site.

5.2.4. Defining key recurrence intervals for tephra impacts on coral reefs

Following the theory of ecosystem recovery, coral reefs naturally return to pre-disturbance state following perturbations (Pearson 1981). There are not many records published that quantify recovery time of coral communities from tephra deposition events. However, benthic surveys in Rabaul Harbour indicate that after initial inhibition by loose sediments (Maniwavie et al. 2001), recovery advanced at previously devastated reef locations within five years (Munday 2000). The complex's overall eruption return rate over the past 250 years was estimated at around 24-60 years (McKee and Duncan 2016). In the Northern Mariana Islands, a time frame of ~90 years for coral reef establishment under volcanic influence was proposed (Houk and Starmer 2010). Based on those records, critical recurrence intervals for tephra deposition on coral reefs were set at a minimum duration of five years, an intermediate time span of 45 years reflecting Rabaul's return periodicity, and at a maximum rate of 90 years.

5.2.5. Probabilistic tephra dispersal modelling

Tephra dispersal models aim at forecasting tephra fallout determined by atmospheric conditions, erupted particle characteristics, as well as the type and intensity of volcanic eruptions in respect to plume height, vertical mass distribution, and other descriptors. A suite of open-source models of variant sophistication and with different utility and purpose exists (Folch 2012). In this study, the well-established and validated Tephra2 model, which uses the advection-diffusion-sedimentation equation to calculate spatial tephra load (Bonadonna 2005;

Bonadonna et al. 2012), was applied. Stochastic sampling of input parameters by code provided in a the Matlab package “TephraProb” (Biass et al. 2016) was used to account for uncertainty in eruption, tephra, and environmental characteristics.

5.2.5.1. Model inputs

A total of 10,000 likely tephra emission scenarios were modelled for each of six eruption intensities according to the Volcanic Explosivity Index (VEI) 2-7 for every volcano (n=137; Fig. 5.1) resulting in more than 8 million simulations. The used inputs are summarised in Tab. 5.2. Plume height was sampled logarithmically as this is more representative, i.e. more small eruption plume heights than larger ones to reflect the observed frequency-magnitude relationships of volcanic eruptions. Conversion of mass into volume indicated outlier pattern from empirical data presented by Mastin et al. (2009). Therefore, uniform mass sampling was constrained to the specified range. Grain size distribution was assumed Gaussian (Biass et al. 2016).

Wind profiles spanning from 01.01.2010 until 31.12.2020 with a temporal resolution of six hour intervals at the locations of each volcano included in this study were retrieved from the European Centre for Medium-Range Weather Forecasts (ECMWF) ERA5 (Reanalysis 5th Generation) data base (Hersbach, et al. 2018). The large number (n=16 072 wind profiles per volcano) was chosen to provide a statistically significant population to account for local atmospheric variations. Given the large number of iterations per modelled eruption scenario wind conditions were randomly selected per run.

Local ground tephra accumulation and respective probabilities were calculated on 10 x 10 km grid cells extending 500 km around each volcano. The simulation was restricted to 500 km, although tephra can travel much further, because the applied model does not account for changes in wind conditions away from the volcano. This leads to reduced confidence in forecast deposition at greater distances (> 500 km) resulting from changes in meteorological patterns (Jenkins et al. 2015). Consequently, the predicted hazard represents a minimum estimate, although only very large eruptions result in significant tephra fallout beyond 500 km (Buckland et al. 2020).

Table 5.2: Overview of intensity-specific Eruption Source Parameter (ESP) settings used for tephra dispersal modelling. The intensity of eruptions is categorized according to the VEI.

VEI [1]	Plume height range (km) [2]	Mass (kg) [3]		Volume (km ³) [4]		Duration range (h) [5]	Grain size (phi) [6]				Diffusion coefficient (m ² /s) [7]	Fall time threshold [8]	
		min	max	min	max		min	mean	max	sd			
2	1 – 5	4.5 10 ⁸	x 1.8 10 ⁹	x	0.00018	0.00072	1 – 6	7	-0.74	-6	2.4	4900	5000
3	3 – 15	8.9 10 ⁸	x 5.7 10 ¹⁰	x	0.000356	0.0228	1 – 12	7	-0.74	-6	2.4	4900	5000
4	14 – 22	4.0 10 ¹⁰	x 6.5 10 ¹¹	x	0.016	0.26	1 – 12	7	0.9	-6	1	8000	9700
5	23 – 31	9.2 10 ¹¹	x 1.5 10 ¹³	x	0.368	6	6 – 12	7	0.9	-6	1	8000	9700
6	30 – 41	1.0 10 ¹³	x 4.7 10 ¹⁴	x	4	188	12 – 24	7	1.35	-6	1.2	8000	9700
7	37 - 45	1.2 10 ¹⁴	x 1.9 10 ¹⁵	x	48	760	12 – 24	7	1.35	-6	1.2	8000	9700

Sources: [1] Newhall and Self 1982, [2] Croweller et al. 2012; Newhall and Self 1982, [3] Mastin et al. 2009, [4] Mastin et al. 2009, [5] Mastin et al. 2009; Newhall and Self 1982, [6] Bonadonna et al. 2005; Volentik et al. 2010; Williams et al. 2020, [7] Biass et al. 2016; Williams et al. 2020, [8] Biass et al. 2016; Williams et al. 2020.

The structure of the openly available Tephra2 and TephraProb code allows parallelisation on a computer cluster to increase computational efficiency (Biass et al. 2016; Bonadonna 2005). Respective scripts were modified in cooperation with Joshua Measure-Hughes and can be found on GitHub (<https://github.com/joshlvmh/tephra2Wrapper>). Model input data preparation and post-processing of outputs was performed with the R software for statistical computing (R Core Team 2022). The code is available on GitHub (<https://github.com/joshlvmh/tephra2Wrapper/tree/main/src/r-processing>). The model was implemented via the high performance computing system of the University of Bristol.

5.2.5.2. Post-processing analysis

Following the methodology used by Jenkins, Magill, et al. (2012), individual scenario simulations were aggregated to produce probability maps, which show the likelihood, for each grid cell, of exceeding any key thickness threshold. Each simulation within a given VEI was considered equally likely so that the simulation probability was simply the annual probability for each simulated eruption intensity divided by the number of simulations of that

eruption intensity (n=10,000). To account for variant annual eruption probabilities the simulated exceedance probabilities per every VEI were multiplied by the respective intensity- and volcano-specific annual eruption probabilities. Consequently, certain scenarios were excluded as not all volcanoes have an eruptive record of all VEI magnitudes. The likelihood values for an eruption of a particular volcano for VEI 2-7 were extracted from the data base presented by Loughlin et al. (2015). To aggregate the VEI-specific probabilities for tephra fallout exceedance of the defined thresholds all probabilities of the individual intensities were summed together per volcano. To derive a combined map depicting the exceedance probabilities of all volcanoes in the study area the volcano-specific probabilities were summed up in a comprehensive raster over the full region. This way, areas impacted more frequently yielded higher probabilities. Aggregated maps of the whole study region were produced for the defined critical threshold values. By combining tephra fallout on a cell-by-cell basis from all possible volcanic sources, rather than from any individual volcano, the probability maps for the study region display the possibility that any grid cell is impacted by tephra from multiple volcanoes. As the selected thresholds concern tephra deposition thickness but the model results quantify tephra load, mass per area was converted to thickness by assuming an average bulk deposit density of 1,000 kg/m³ (Crosweller et al. 2012; Pyle 1995).

5.3. Results

Key results of this study comprise the informed selection of critical thresholds of tephra deposition on coral reefs. The model results are displayed showing spatial gradients of such hazards in the wider CT region and furthermore quantifying which fractions of regional coral reefs are most likely affected at which rates of volcanic disturbance recurrence.

5.3.1. Coral reef responses to tephra deposition

There is a decrease in live coral cover with increasing tephra deposition This is the case for both, spatial and temporal, reference sites (Fig. 5.2).

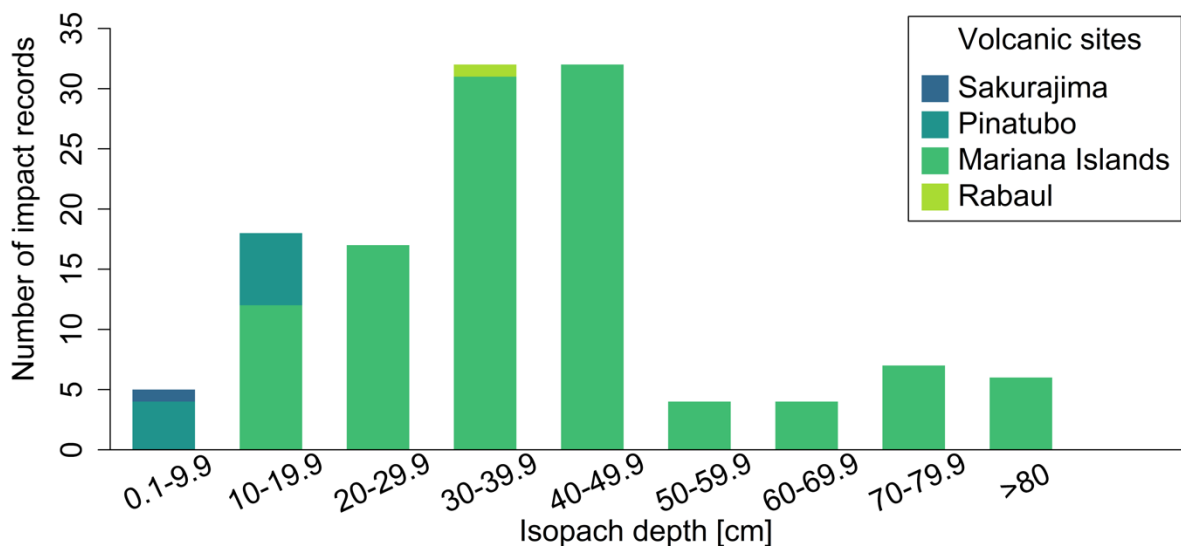
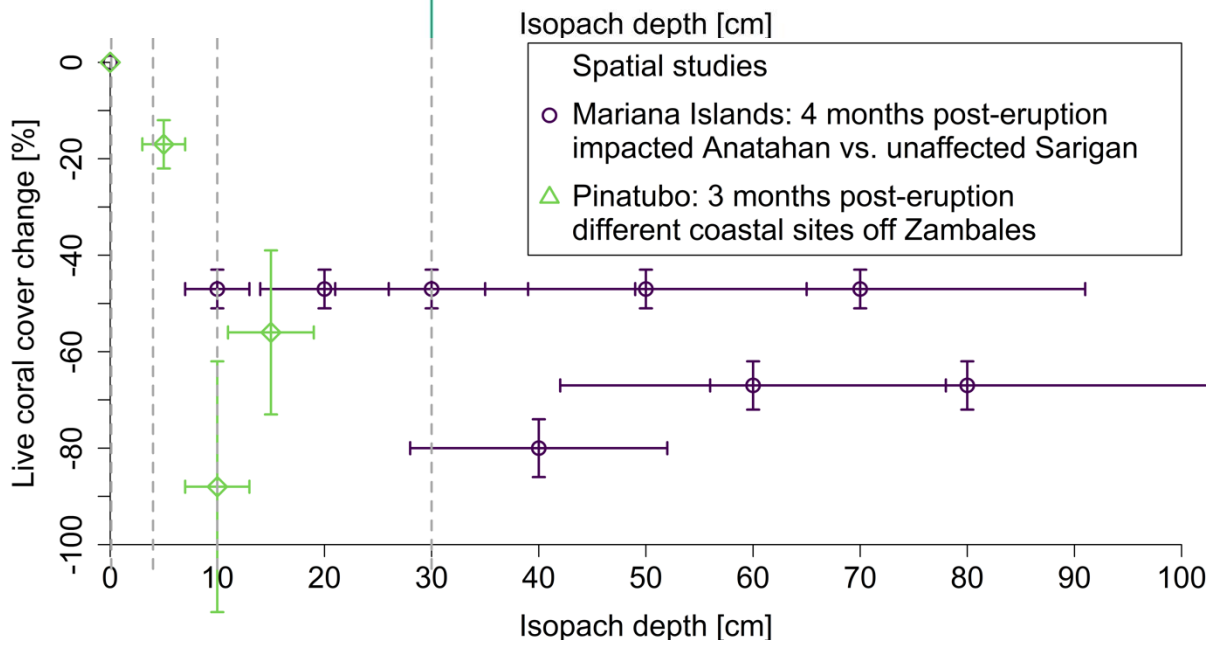
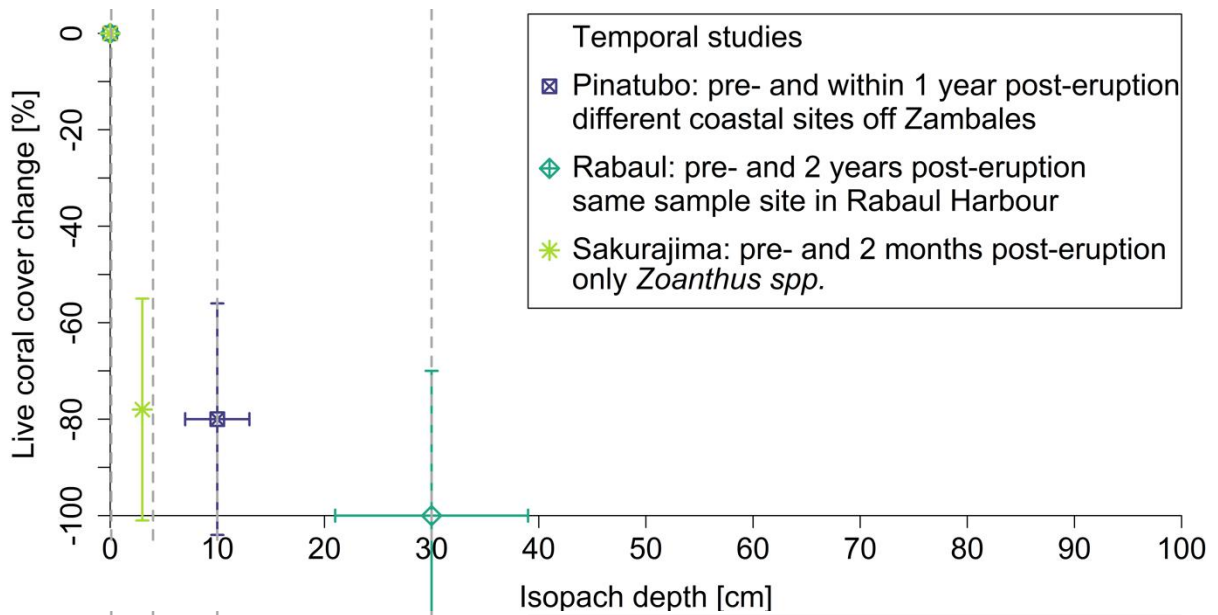


Figure 5.2: Percent of live coral cover change and associated tephra deposition at impacted reefs following four eruptions: Sakurajima in 1982, Pinatubo in 1991, Rabaul in 1994, and Anatahan in 2003. In cases of multiple records of coral cover change at the same isopach depth, the median live coral cover change was calculated. Top: Temporal changes of live coral cover before the impact with no live coral cover change without tephra fallout to post impact states all at the same location (Maniwavie et al. 2001; Ono et al. 2002; Pajaro et al. 1992). Middle: Spatial studies across different reef sites showing live coral cover variations with different levels of tephra deposition (Atrigenio et al. 1991; Ochavillo et al. 1992; Vroom and Zgliczynski 2011). All isopach depths are terrestrial sea level-based estimates. Uncertainties are displayed by respective error bars indicating natural variations in isopach thickness estimates (Engwell et al. 2013) along the x-axis and observed deviations of live coral cover assessments along the y-axis. The grey vertical dashed lines show the selected thresholds for critical changes in live coral cover under 0.1, 4, 10, and 30 cm tephra deposition. The coral cover estimates from Kagoshima Bay off Sakurajima volcano (yellow stars) are of a single species of *Zoanthus* sp.; all other records represent overall benthic coral cover. Bottom: Numbers of coral cover records binned per isopach level from the four different volcanic sites where impacts from tephra deposition on coral reefs are reported.

For temporal studies (n=3) change rates appear rapid, with live coral cover losses of ~75-100% at relatively thin to moderate tephra isopach levels of 4-30 cm (Fig. 5.2). Coral reefs affected by tephra deposition from the Pinatubo eruption in 1991 show a decrease in live coral cover by 80% at 10 cm of volcanic material deposition within a year after the eruption. The cover of *Zoanthus* sp. was similarly reduced in Sakurajima within two months post eruption. In this case, just 4 cm of tephra layer caused this change. In Rabaul Harbour, coral reef formations were not present after two years of tephra fallout in the natural basin at 30 cm isopach depth.

Spatial studies reveal more moderate and variant responses of coral cover development as a consequence of tephra influx. In the Mariana Islands differences of 45-80% in reduced live coral cover were observed under tephra deposition ranging from 10-80 cm in isopach depth by comparing the affected island Anatahan with the unaffected neighbour island Sarigan. Along a spatial gradient off Zambales' coast in the Philippines with 0 cm, 5 cm, 10 cm, and 15 cm tephra fallout declines rates of 15-90% live coral cover reduction were detected.

The available data set of coral cover change as a function of volcanic material fallout is by far the most extensive from the Mariana Islands followed by coral reefs impacted from Pinatubo's eruption, which were subject of several studies. The available records from Rabaul and Sakurajima represent only single data points (Tab. 5.2).

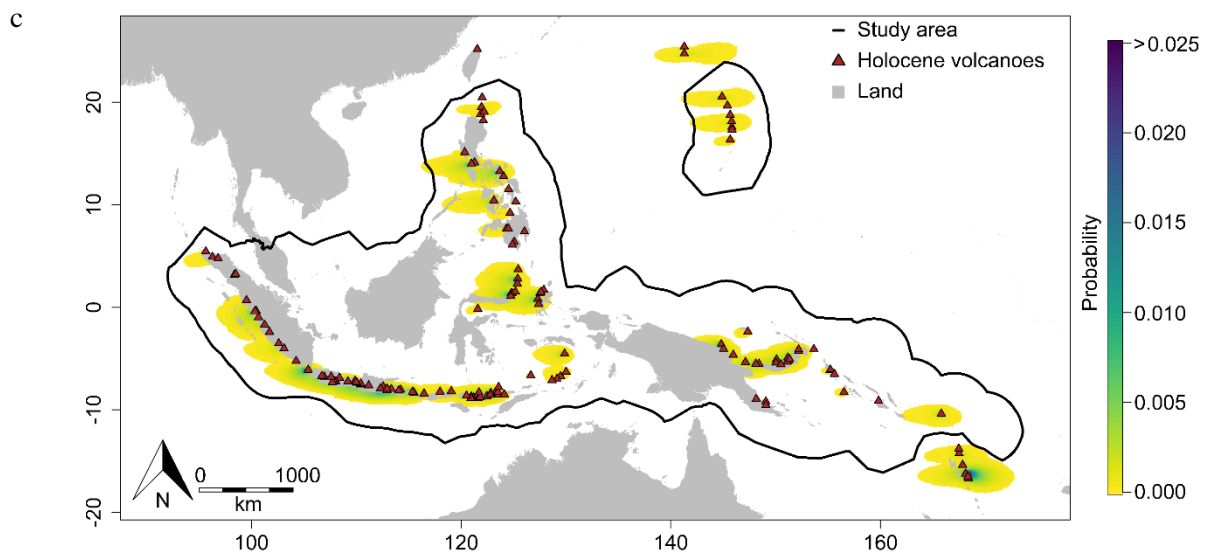
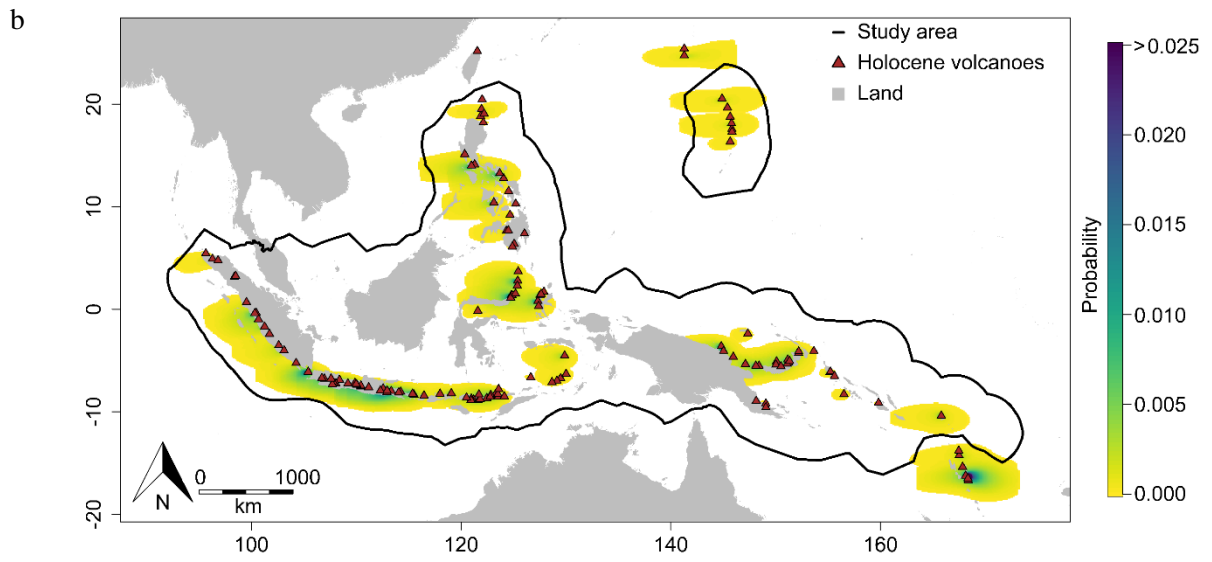
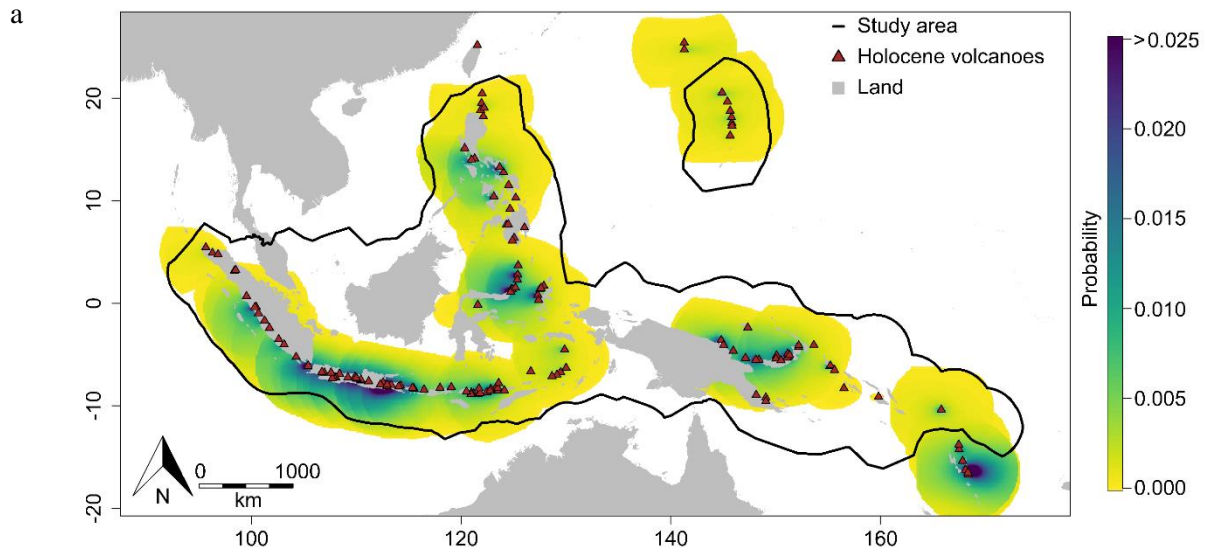
5.3.2. Defining tephra thickness thresholds for coral cover change

Four key tephra deposition thresholds at 0.1, 4, 10, and 30 cm isopach depth referring to 1, 40, 100, and 300 kg/m² area density deposition were chosen based on the following observations:

- Coral mortality from overgrowth by the cyanobacteriosponge *Terpios hoshinota* was detected around Pagan Island (Northern Mariana Islands) in 2009-2010 coinciding with light tephra and gas emissions. Volcanic ocean water fertilization was identified to cause the observed coral health deterioration (Schils 2012). With those adverse effects detected from minor tephra exposure, a trace threshold of 0.1 cm (1 kg/m² load) was selected. That value is commonly referred to as a minimum threshold with implications of tephra fallout on transport and infrastructure e.g., airport closure (Houghton et al. 2006).
- Isopach depths of 4 cm (40 kg/m² area density) tephra deposition caused ~80% losses of *Zoanthus* sp. in Kagoshima Bay after an eruption of nearby Sakurajima in 1982 (Ono et al. 2002) (Fig. 5.2). Furthermore, the diversity of foraminifera assemblages differed significantly at sites with high tephra deposition thickness close by the vent (> 3 cm) compared with more distal locations with lower volcanic material accumulation. Foraminifera were found resilient under limited material deposition (< 2 cm) without observed community alterations (Hess et al., 2001).
- Relative live coral cover losses up to 50-90% were detected under 10 cm (100 kg/m²) tephra deposition in the coastal fallout zone following Pinatubo's eruption in 1991 (Ochavillo et al. 1992; Pajaro et al. 1992) (Fig. 5.2).
- 30 cm (300 kg/m²) was the minimum tephra deposition rate to cause 100% live coral cover reduction at Anatahan four months past the eruption in 2003 (Vroom and Zgliczynski 2011). Moreover, complete coral destruction in Rabaul Harbour was caused by a comparable isopach depth (Maniwavie et al. 2001) (Fig. 5.2).

5.3.3. Spatial patterns of tephra deposition probabilities

Hazard probabilities over the whole study region were compiled by combining all model outputs at the specified threshold values. Spatial display of the overall accumulative probability of any location in the CT being affected by tephra deposition from any volcano in the region reflects the location of volcanic hotspots along the Sunda Arc, in North Sulawesi, in the Central Philippines, in New Britain, and in north-eastern Papua New Guinea around the Bismarck Sea. The impact zones reflect the hazardous thresholds. The greatest area is affected by 0.1 cm material deposition whereas significantly smaller locations in direct vicinity to volcanic vents are impacted at very low probabilities by destructive tephra fallout rates of 30 cm at reef scale (Fig. 5.3).



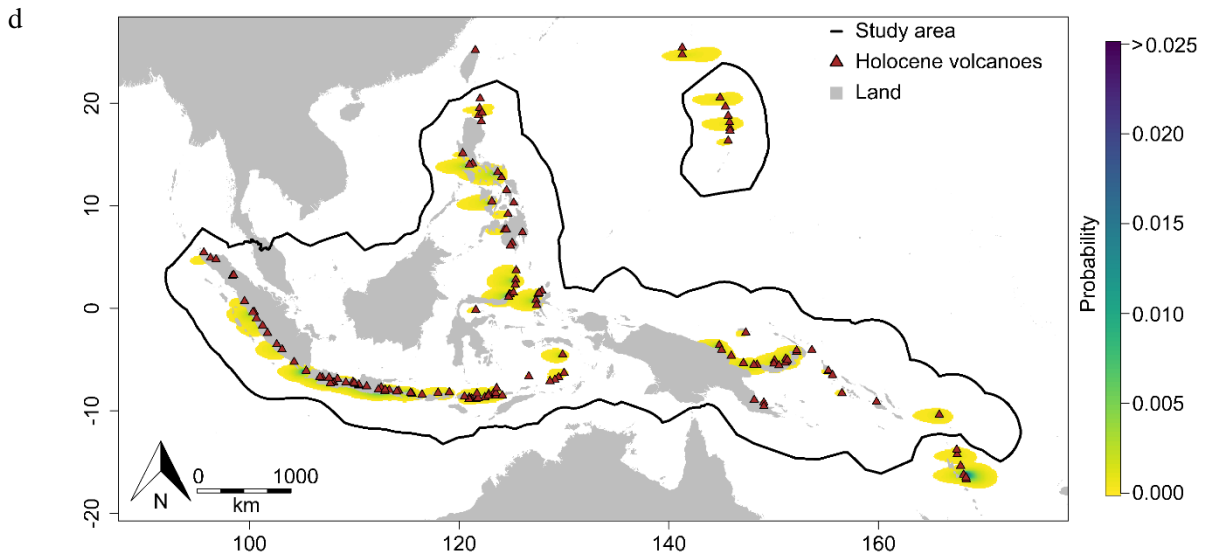


Figure 5.3: Probability maps of exceedance of tephra isopach depth thresholds. a) 0.1 cm isopach depth, b) 4 cm isopach depth, c) 10 cm isopach depth, and d) 30 cm isopach depth.

5.3.4. Recurrence intervals

The percentage of coral reefs impacted at each tephra deposition thickness threshold, as a function of the average recurrence interval (ARI), is presented in Fig. 5.4.

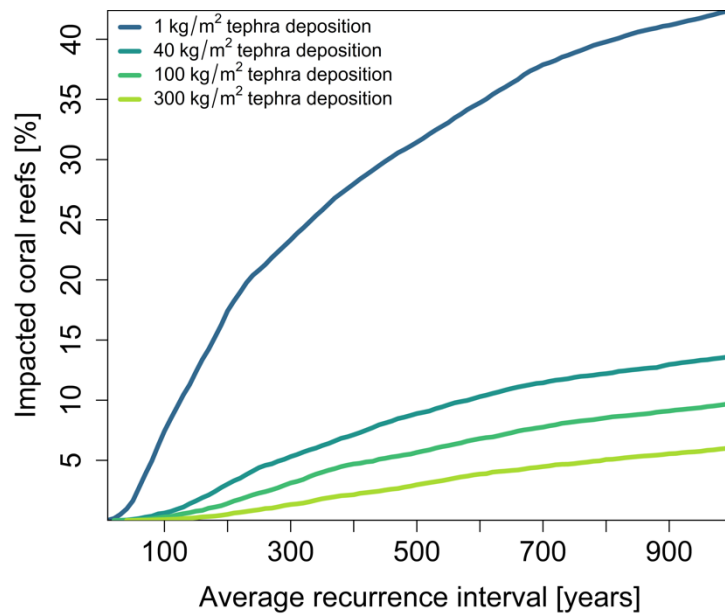


Figure 5.4: Average recurrence intervals of variant hazard intensities to affect coral reefs in the Coral Triangle (CT).

While higher deposition rates of 40, 100, and 300 kg/m² show an almost parallel but shallow increase, the fraction of coral reefs potentially affected by trace tephra fallout of 1 kg/m² rises more steeply and hump-shaped with over 40% of coral reefs in the CT being most likely affected over the course of a millennia. The percentage of potentially affected coral reefs is

lower in the cases of higher depositional loads: 14%, 10%, and 6% of coral reefs in the region are prone to deposition of 40, 100, and 300 kg/m² tephra respectively. While all trends are increasing, the highest load shows an almost linear growth whereas the trace deposition is following a curve-shaped increase. Until an average recurrence interval below 100 years, the percentage of potentially affected coral reefs is just varying marginally between tephra loads of 40, 100, and 300 kg/m².

5.4. Discussion

Setting the results of probabilistic tephra hazard modelling in the CT into the context of contemporary scientific knowledge is essential to deduce novel insights on the effects of tephra fall hazards affecting coral reef ecosystems. Therefore, the findings of this study are discussed in this section.

5.4.1. Coral reef responses to tephra deposition

Empirical data shows that tephra deposition results in reductions of live coral cover in tropical shallow-water coral reef ecosystems. This causal relation is confirmed by the findings of both, temporal and spatial studies linking tephra deposition to isopach depth (Fig. 5.2). The observed physical implications from settling of tephra blankets onto coral reefs are manifold. Corals and other reef organisms are partially or entirely affected by mortality from burial under deposits, dislocation, physical damage to tissues and skeletal structures, particle inclusion and resultant growth anomalies, stress symptoms, nuisance species spread, and habitat deterioration (e.g., Eldredge and Kropp 1985; Heikoop, Tsujita, Heikoop, et al. 1996; Houk 2011; Maniwavie et al. 2001; Reuter and Piller 2011; Schils 2012; Tomascik et al. 1996; Vroom and Zgliczynski 2011) (Tab. 3.1). This is detailed in chapter three of this thesis.

Reductions of live coral cover by 80-100% 1-2 years after volcanic activities at the same locations where pre-disturbance assessments have been undertaken were found in the impact zones of Pinatubo and the Rabaul volcanic complex (Fig. 5.2). This indicates that firstly, tephra deposition causes direct mortality to corals, and secondly, habitat conditions remain in poor ecological state inhibiting coral reef regeneration in the aftermath of eruptive activities. Ongoing erosion of volcanic materials, redeposition, and resuspension are potential underlying factors resulting in substrate instability which is unsuitable for coral settlement. In Rabaul Harbour, coral regrowth was only found on solid and stable surfaces at former reef locations that were smothered by deep tephra deposition (Maniwavie et al. 2001). This

underlines the importance of suitable substrate structures for coral reef formation and regeneration. Such specification on substrate characteristics is not detailed in the case of the temporal record from the reefs impacted by Pinatubo. However, downstream sedimentation, redeposition of pyroclastic materials, and lahars reported for years after the eruption (Janda et al. 1996; Rodolfo et al. 1996; van Westen and Daag 2005) indicate that similar to the situation in Rabaul, reef substrate conditions in coastal zones impacted by Pinatubo were adverse for coral settlement after the eruption. Similarly, cover reductions of *Zoanthus* sp. by around 80% caused by volcanic material fallout in Kagoshima Bay from an active cone of nearby Sakurajima was linked with changes in substrate composition and stability (Ono, Reimer, and Tsukahara 2003). Those findings indicate that loose benthic substrates from volcanically-induced habitat changes may constitute the major constraint to reef development in areas of potential tephra deposition.

Spatial studies, which represent coral cover assessments over a gradient of impact intensity, also reveal decreases in coral cover under tephra deposition (Fig. 5.2). Along the coastal zone of Zambales, which was affected by the Pinatubo eruption in 1991, coral cover was up to 84% lower when impacted by volcanic material fallout compared to a reference site without material deposition. Coral cover estimates at 5 cm, 10 cm, and 15 cm isopach depth all show a decline with variance in impact magnitude in live coral cover loss (Atrigenio et al. 1991). Similarly, the observational records from Anatahan in comparison to coral cover estimates from the unaffected neighbour island Sarigan show that tephra deposition causes decreasing live coral cover. The data set from the Mariana Islands is the most extensive of all studies (Tab. 5.1, Fig. 5.2). This catalogue exhibits great variance in the biotic coral response to volcanic disturbances. While no living corals were found at one site with 30 cm isopach depth, even higher material load did not necessarily eliminate all sessile benthic organisms at other locations (Fig. 5.2). This points to the importance of environmental site conditions to either mitigate or even enhance destructive volcanic impacts. Wave energy is mentioned as such a factor to counteract the disturbance effect by clearing off tephra sediments (Reuter and Piller 2011; Vroom and Zgliczynski 2011). Contrarily, heavy and constant wave exposition may also inhibit the regeneration of coral reefs under the influence of tephra redeposition by imposing a permanent physical disturbances and causing substrate instability (Tomascik et al. 1996). This illustrates the duality of effects abiotic habitat factors impose on coral reefs under volcanic influence. Another environmental factor determining the severity of tephra deposition on coral reef organisms is bottom relief. Slope inclination is crucial for sediment

retention. Thus corals on steep slopes are rather damaged but not buried by tephra. This allows for faster regrowth from colony remnants (Maniwavie et al. 2001). As a consequence, the original structural habitat heterogeneity is a predictor of volcanic impact severity at reef scale.

It should be noted that only one of the reviewed studies, the assessment of *Zoanthus* decline in Kagoshima Bay, provides data on isopach thickness measured directly on the reef (Ono et al. 2002). For all other studies, tephra deposition records were derived from primarily terrestrial isopach maps. While this procedure causes additional uncertainty, such an approach is pragmatic in terms of hazard quantification. There is no way to account for dynamics within the water column and potential effects of water depth on depositional loads on the seafloor. However, results from marine sediment trap analyses indicate that ocean currents have minor effects on submarine tephra fallout with rapid vertical settling caused by water adsorption of particle aggregates (Wiesner et al. 1995). Distinction of live coral cover reduction under tephra deposition at different water depth levels is made by just one study (Pajaro et al. 1992). In this case of a temporal gradient comparing pre- and within one year post-eruption rates of live coral cover loss between 3 and 10 m water, depth seems to be not significantly affecting the rate of coral reduction. The decline varies just by 3.3% between the two different depth levels. This indicates that opposing to the effects of wave impacts, potential perturbations of tephra fallout in the aquatic sphere are neglectable at reef scale.

Apart from site-specific environmental factors, species-specific responses and abilities to tolerate volcanic hazards from tephra exposure essentially determine impact patterns among biotic communities. Records of massive decreases in *Zoanthus* sp. cover resulting from tephra fallout highlight the destructive potential of tephra deposition at species level. *Zoanthus* are encrusting anemone-like cnidarians. They form colonies on hard benthic substrates and are widely distributed in coral reef ecosystems from tropical to temperate waters (Ono et al. 2002, 2003). In Kagoshima Bay, volcanic material fallout was found detrimental to *Zoanthus* colonies over time scales from months to decades (Ono et al. 2003). Such a drastic loss of encrusting soft corals points to species-specific responses within reef communities. Due to less skeletal stability and structural complexity, soft corals are expected to be more sensitive to physical impacts compared to hard coral i.e. Scleractinia. Therefore, the observed response of *Zoanthus* is a valuable record for assessing impact thresholds on vulnerable species in a coral reef community. Furthermore, differences in decline rates

among four functional groups of coral reef organisms varying from factors 1.4-3.0 (Vroom and Zgliczynski 2011) most likely reflect variant physiological resilience under volcanic disturbance exposure. While mobile reef organisms (e.g., fish, foraminifera) have a chance to flee or self-extract from volcanic material deposits (Eldredge and Kropp 1985; Hess et al. 2001; Ochavillo et al. 1992), stony reef-forming corals lack such abilities and cannot evade impact zones.

For sessile corals, morphology, individual colony size, abilities of physiological adaptation or tolerance, and abundance are important factors to determine survival rates among different species. At Pagan Island, coral morphological growth form was linked with survival rates of individual genera. Massive species, such as *Porites*, showed little signs of damage (e.g., skeletal breakage) from volcanic material deposition, whereas branching corals were severely affected. The openness of the colony canopy was found critical as sediment retention is dependent on the morphological structure. Growth types with open and widely-spaced branches were less affected in comparison to dense branching colonies, like *Acropora* (Eldredge and Kropp 1985). While there are speculations about very large massive corals within tens of kilometres from the vent surviving the extreme eruption of Tambora in 1815 (Best et al. 1989), the size of individual colonies is certainly important in terms of coral susceptibility and survival rates. Unaffected parts of larger colonies that protrude out of the volcanoclastic material can remain alive despite partial burial, removal, and basal sections being buried by tephra (Maniwavie et al. 2001; Pandolfi et al. 2006; Reuter and Piller 2011; Vroom and Zgliczynski 2011) or lava effusion (Moore et al. 1990). Therefore, size matters when it comes to individual coral colony survival under volcanic influence. Looking at the difference in impacts among different genera of corals in the aftermath of Anatahan's eruption in 2003, it was speculated that great abundance was beneficial for the persistence of certain species. In the Mariana Islands, *Porites* are widely distributed and occur in great numbers. This could explain their relatively high rates of persistence under tephra exposition (Vroom and Zgliczynski 2011).

However, despite clear evidence of species-specific coral responses to tephra fallout, empirical data from field surveys is limited. Only one of the identified key studies quantitatively relates tephra hazards to an individual species response (Ono et al. 2002). All other sources refer to "coral cover" without greater taxonomic specification. This should be considered when interpreting the presented decline rates from temporal and spatial studies.

Despite lacking species differentiation, live coral cover might be even more suited to assess ecosystem effects than individual species responses. The reference coral reef communities of the consulted studies are located in the CT (Fig. 1.1). Those reefs are typically characterized by high coral species richness (Hoeksema 2007; Veron et al. 2009). Therefore, a broad range of functional types and individual sensitivities is represented by overall coral cover. The fact that still up to 100% of live coral cover is eliminated in different instances (Fig. 5.2) indicates an overall susceptibility of the entire functional and taxonomic coral community. This could, in its full extent, not be represented by data on single species responses to tephra deposition. However, following up upon a brief explanation for different coping abilities of certain coral genera presented by Vroom and Zgliczynski (2011), further research on coral species-specific responses to volcanic hazard exposure could yield novel insights. Another point for the validity of coral cover as a representative unit to quantify ecological implications from tephra deposition on coral reefs is that it is widely used and relatively easy to assess. The percentage of live coral cover per area is a well-accepted standard in coral reef management and research. Which exact number at any particular location is representative of an ecologically optimal coral reef state in terms of diversity, resilience, and health is to be discussed elsewhere. However, it should be noted that according to the intermediate disturbance hypothesis coral cover is negatively correlated with species diversity (Rogers 1993). Projecting this to the presented results indicates that high coral cover rates do most likely not represent highly biodiverse communities. Anyway, to account for the unknown baseline of live coral cover under ideal conditions, relative changes were used in the presented study.

Coral cover naturally changes over time with individual species growing as well as competition and disturbances continuously changing community composition and diversity. This is especially true for coral reefs under the influence of volcanic activities (Grigg and Maragos 1974; Jouval et al. 2020). Respective considerations to compensate such temporal variations in the reviewed records were not possible as this would require detailed and long-term ecological assessment of the reef condition. However, despite the limited number of seven studies this diversification should attenuate the additional uncertainty from natural fluctuations to a given extent. Fast coral regrowth from remaining colony remnants within two years after complete reef destruction, like observed in Rabaul Harbour following the 1994 Tavurvur eruption (Maniwavie et al. 2001), highlights the extreme temporal dynamics in live coral cover change over time at volcanically-affected reef sites. Such great variation in coral cover within a few years matches observations from other coral reefs under

disturbances influences, like e.g., mass-bleaching events in northern Australia (Smith, Gilmour, and Heyward 2008).

Corals are important ecosystem engineers providing habitat for a variety of reef-associated organisms (Wild et al. 2011). Looking at the fate of diverse reef functional groups under volcanic hazard exposure outlines the fundamental role corals have in terms of habitat characterization within benthic reef ecosystems. In areas exposed to tephra deposition from Pinatubo's eruption in 1991, fish biomass was positively related to live coral cover – the more coral, the healthier the fish stocks (Ochavillo et al. 1992). Testing for correlation between coral cover representing colony health status and the condition of other reef functional groups might allow projection of observed declines in live coral cover under volcanic hazard exposition unto other marine taxa. Such an approach could allow derivation of novel insights on the effects volcanic hazards potentially impose on a broad range of marine organisms. This could be subject of future investigations.

Despite the destructive potential and strong decline rates in live coral cover under tephra deposition, coral reefs are not entirely eliminated at ecosystem scale (Eldredge and Kropp 1985; Tomascik et al. 1996; Vroom and Zgliczynski 2011). The observed variance in ecological response of the empirical data (Fig. 5.2) could be a function of firstly, environmental habitat heterogeneity at reef scale that determines local impact severity, and secondly, biotic and functional diversity within the coral reef community affected by tephra fallout.

5.4.2. Defining critical thresholds for coral reef responses to tephra deposition

Variance in spatial records relating tephra fallout to changes in the coral community reflects differences in site-specific environmental conditions that affect tephra deposition on coral reefs. Therefore, temporal records provide more robust of a reference frame in comparison to spatial studies that relate tephra deposition to live coral cover change. Looking at the observed decline rates and the differences in biotic reef responses to tephra fall hazards, temporal studies provide a clear trend to ultimately inform the setting of critical threshold values (Fig. 5.2). However, notwithstanding the bias of variant habitat conditions at different locations, spatial references constitute valuable additions to a scarce data set helping for improved definition of critical tipping points in ecological responses.

The smallest threshold to mark a critical value for impacts on corals from tephra exposition was set at 0.1 cm isopach depth (1 kg/m^2 area density). Such a light hazard intensity is reported not to result in direct physical impairment from material deposition, but potentially to induce chemical alterations to ocean water quality that ultimately affect corals at reef scale. Nuisance species spread of cyanobacteriosponges was found during periods volcanic activities with light tephra and gas emissions from Mount Pagan in the Northern Mariana Islands. The detected overgrowth of scleractinian corals by *Terpios hoshinota* was linked to volcanic ocean water fertilization (Schils 2012). Biological productivity in aquatic ecosystems is typically limited by certain nutrients. If those essential nutrients are provided via volcanic material influx, algae benefit from their abilities to rapidly take up the available resources (Achterberg et al. 2013; Lin et al. 2011). Under such eutrophic conditions, ecological dominance in reef ecosystems may temporarily shift from corals to algae (Bell 1992). Therefore, setting a minimum trace threshold for coral implications from light hazards is crucial to account for the outlined disturbance effects.

Isopach levels of just few centimetres were found causing direct negative effects to marine organisms. Minor tephra deposition resulted in ~80% decline in *Zoanthus* sp. (Ono et al. 2002) (Fig. 5.2), growth of branching coral was terminated within fringing and barrier reef communities (Pandolfi et al. 2006), foraminifera showed changes in community composition as a result of tephra fallout (Hess et al. 2001), and tephra deposition was reported to impose mortality among fishes in various different instances (Blong 1984b). Apart from implications imposed by smothering from volcaniclasts, such deposition rates typically affect ocean water properties with changes in pH and increased turbidity (Blong 1984b). To account for such impacts at ~3-4 cm isopach thickness, a critical threshold for tephra exposure was set at 4 cm (40 kg/m^2 material load) deposition. This tipping point represents the state at which certain individual species or functional groups of coral reef organisms with limited resilience are severely affected. Such adverse effects may result in instability of the ecological community composition.

Tephra fallout of 10 cm thickness is a common benchmark for minor damage to natural vegetation and agricultural production (Blong 1984b). At this given hazard intensity, relative losses in live coral cover of 50-90% were detected among coastal coral reefs in the impact zone from Pinatubo's activities in 1991 (Ochavillo et al. 1992; Pajaro et al. 1992) (Fig. 5.2). The loss of almost the entire live coral cover by decrease of up to 90% indicates that several

coral species and morphological types suffer from the volcanic hazard. Such volcanic material fallout results in complete burial of encrusting growth forms and small individual colonies. Furthermore, basal parts of massive, branching, and tabular coral species get covered under tephra deposits. Thus, 100 kg material load per square meter was defined as the next critical value.

The smallest reported value of tephra fall to completely eliminate all coral cover at a local scale was 30 cm. The critical tipping of 300 kg/m² causing full reef destruction was deduced from both, temporal and spatial studies in Rabaul Harbour (Maniwavie et al. 2001) and at Anatahan (Vroom and Zgliczynski 2011) (Fig. 5.2). Following a conservative approach, this threshold at which all coral cover might be lost can be seen as the ultimate indicator for coral community susceptibility to volcanic material exposure. At this isopach depth, corals of any growth form are affected by burial and deep tephra beds prevent regrowth due to substrate instability. Furthermore, at depositional rates greater 10 cm, compounding potential impacts from volcanic activities include pumice drift, particle dissolution, and water turbidity (Atrigenio et al. 1991; Maniwavie et al. 2001; Ochavillo et al. 1992; Vroom and Zgliczynski 2011). However, notwithstanding these tremendous physical and environmental implications, large colonies partially extending beyond the disturbance horizon may still remain intact (Pandolfi et al. 2006; Reuter and Piller 2011).

As options to define critical thresholds of coral change caused by tephra deposition were reviewed, potentially alternative approaches were identified. Derivation of such crucial values from experimental studies was applied with different thematic focus (e.g., Spence et al. 2005; Stewart et al. 2006) but investigations on coral responses to tephra exposure under laboratory conditions were not undertaken to date. However, such approaches might produce valuable insights in specific biotic and ecological coral responses to variant levels of tephra deposition under variant environmental site conditions.

Multiple nonlinear regression analysis methods including spline regression, linear and polynomial regression analysis, and generalized additive models were checked to fit the observed live coral cover rates with levels of tephra fallout. However, the significance of statistical operations is limited by the small number of observational records. This results in huge uncertainties of predictions. There is also a risk of mathematically predicting negative isopach thickness, which is a practical impossibility. Data interpolation via Bayesian belief networks to represent conditional relations between multiple variables could be used for

reconstruction of causalities among the input variables (Tang and McCabe 2007). Therefore, this approach is theoretically more suitable for detection of driving factors and for ranking of individual predictive importance regarding certain responses. However, this approach is again limited by few records in the original data set. Ultimately, the option of a moderated expert consultation including both disciplines of coral reef ecology and volcanology could be another option to identify critical thresholds of coral cover change under tephra deposition and thus overcome the inherent limitation by a small data archive. Future work in the field of volcanic hazard assessment to coral reefs would greatly benefit from such an advancement.

5.4.3. Spatial and temporal extent of tephra deposition on coral reefs

Probabilistic tephra hazard simulation in the CT indicates that over the course of one millennia, 42% of all coral reefs in the region are most likely affected by 1 kg/m² tephra deposition. The percentage of potentially impacted coral reefs decreases with increasing hazard intensity: 14% of the regional coral reefs are prone to deposition of 40 kg/m² tephra, a hazard intensity with the potential to affect multiple coral species (100 kg/m² material deposition) most likely affects 10% of coral reef in the CT, while 6% of all coral reefs in the region may be impacted by fatal tephra deposition rates of 300 kg/m² (Fig. 5.4). Relating the different hazard intensities to documented time periods needed from coral reef recovery from tephra deposition is an essential step to derive insights on the extent of reefs at risk to volcanic perturbations.

Coral reef recovery from exposure to trace tephra deposition was found occurring rapidly with almost instant reversal to pre-disturbance state after cessation of underlying volcanic activities driving the observed ecological changes (Schils 2012) (Fig. 4.2). Therefore, hazard intensity at the lowest threshold deposition of 1 kg tephra per square meter is very unlikely to cause long-term alterations to the ecological condition of coral reefs in the wider CT region. Despite the broad distribution throughout the region (Fig. 5.3 a), not even half of the coral reefs are in fact at risk of such a volcanic perturbation. However, 42% of all coral reefs in the region may be affected at least once per 1,000 years. As corals exposed to continuous non-volcanic stressors, such as ocean water warming, were found more susceptible to abrupt volcanic hazards (Wu et al. 2018), volcanic disturbances might be increasingly critical to coral reef health in the CT when considering current projections of climate change effects (McManus et al. 2020). Considering the increasing thermal pressure predicted to drive coral reef decline in the future, effects of combined multi stressor exposition including volcanic

disturbances may be significant in shaping coral reef communities in the CT over the coming centuries. Future research will show how implications from tephra deposition might fit into the disturbance regime to tropical shallow-water coral reefs under future scenarios of ongoing climatic changes.

For direct physical impairment from tephra deposition onto coral reefs, recover rates vary significantly according to site-specific habitat conditions. Recolonization occurred rapidly in Rabaul Harbour where corals were found regrowing on solid surfaces in tephra fallout zones as well as along steep submarine slopes with little sediment retention within two years after the eruption event (Maniwavie et al. 2001). In contrast, no reef formation in coastal deposition zones along Lombok's eastern coast happened over 750 years after the extreme eruption of Samalas (Mutaqin 2020). This hints to the superior role of suitable habitat conditions being more important to determine coral recovery from tephra hazards compared with initial disturbance severity. If solid benthic surface are available and water properties have normalised from volcanic material deposition, corals will regrow fuelled by adjacent resource populations. Opposingly, recolonization may be suppressed over centuries if habitat conditions at reef scale do not return to a state of environmental habitat parameters that is suited for coral persistence.

Considering that according to the underlying tephra fall modelling 14% of the coral reefs in the wider CT region are prone to hazard exposition that might severely eliminate certain reef functional groups, like e.g., soft corals, illustrates the vulnerability of coral reefs to volcanic disturbances. Loss of particular taxa means lower species diversity, which can lead to reduced ecological resilience and productivity. The role of tephra deposition to change coral reef species composition by filtering out certain species and genera with limited tolerance abilities is evident (Eldredge and Kropp 1985; Vroom and Zgliczynski 2011). However, further trajectories are unclear. In contrast to lava flows, which, at moderate disturbance frequency, can even enhance coral diversity (Grigg and Maragos 1974), no such development is documented for tephra-impacted reef sites. This is a consequence of lacking long-term ecological data to monitor recolonization of respective impact sites. While no positive effect from tephra fallout on coral species diversity was proven yet, higher rates of tephra accumulation have the potential to severely impair different taxa. Every 1,000 years 10% of the CT's coral reef are likely afflicted by deposition rates of 10 cm vertical accumulation

(Fig. 5.4). This imposes a severe threat of functional reef degradation and loss of ecological integrity.

Evidence of complete termination of biogenic reef carbonate production from extreme tephra deposition is rare. However, examples of such drastic effects are known from multiple sites in the CT (Mutaqin 2020; Pandolfi et al. 2006). This reflects the findings of the underlying analysis. Temporally and spatially, the probability of high tephra loads with fatal consequences to entire coral reef communities is low in the CT. Just 6% of all coral reefs might over the course of a millennia be subject to complete destruction from tephra deposition (Fig. 5.4). This however, shows that tephra fall hazards impose a realistic threat to coral reef persistence within a limited spatial and temporal extent. Such hazard magnitudes typically originate from large individual eruptive events. Despite their probability weighted contribution to tephra falls being minor, these large magnitude activities can be important contributors to severe impacts seen on corals (Atrigenio et al., 1991; Ochavillo et al., 1992; Pajaro et al., 1992). In the study region, diverse examples of such large eruptions are documented including Samalas' eruption in 1257 and Tambora's eruption in 1815, both with VEI 7 to justify inclusion of such extreme events.

The presented results allow risk quantification enabling comparison with other local threats to coral reefs. With 6%, 10%, and 14% of coral reefs in the CT potentially affected by complete destruction, multiple species elimination, and single species exclusion respectively, volcanic hazards from tephra deposition rank above marine-based pollution and damage to coral reefs in a comprehensive risk quantification presented by Burke et al. (2012; Fig. ES-2). Other local stressors imposing higher risks to coral reef degradation compared to volcanic impacts include coastal development, pollution from terrestrial watersheds, and overexploitation of marine resources. Notwithstanding the limited significance of volcanic perturbations compared with those disturbances, the presented results suggest consideration of volcanic perturbations to coral reef ecosystems in regional monitoring and management protocols, which is typically not the case.

By any consideration of the presented probability maps of hazard exposure to the four selected thresholds (Fig. 5.3), it should be noted that there are a few limitations associated with the applied modelling approach. The validity of results from semi-analytical tephra dispersal models, like Tephra2, is constrained for low-magnitude eruptions with low vertical plume extension because relevant topographic effects are neglected in this methodological

approach. Tephra transport over large distances cannot be described with precision as the assumption of homogeneity in wind conditions is not realistic over large spatial scales and for prolonged time periods (Bonadonna et al. 2005, 2012; Folch 2012). Yet, uncertainty analyses of numerical tephra dispersal modelling were in good accordance with field records (Bonadonna 2006). This indicates the suitability and reliability of the applied methodology. Ultimately, despite all model limitations the results derived from the described probabilistic simulation are a best estimate to quantify tephra hazards to coral reefs in the CT with state-of-the-art procedure.

Looking at spatial variations of tephra hazards to coral reefs in the CT reveals impact severity from tephra deposition as a function of spatial vicinity to single or multiple active volcanic vents. Another important factor to determine the simulated spatial patterns is the direction of prevailing wind patterns (Fig. 5.3). This is particularly obvious along the Sunda Arc in Java and Sumatra where volcanic plumes bend in southwestern to western direction. In New Britain, the Banda Arc, North Sulawesi, and the Central Philippines, deposition is found primarily west of the vents. There was no distinction undertaken in monsoonal wind regimes. So the modelled tephra fallout patterns represent the average of prevalent wind directions in the region.

Local hotspots in tephra hazard exposure are located around the region's volcanic hotspots. Highest impact from tephra fall are predicted for the southern coastline of the Sunda Arc, in North Sulawesi, with some discontinuity in the Central Philippines, and in New Britain. In those zones, cumulative effects from impacts originating from multiple volcanoes contribute to respectively elevated hazard probabilities. Hazards from individual volcanoes occur in the Banda Arc and in the eastern Solomon Islands (Fig. 5.3).

Comparing the derived hazard maps with the spatial distribution of coral reefs in the CT confirms that volcanic tephra impacts do not exclude corals reefs at a larger scale (Fig. 1.1, Fig. 5.3). Well-developed and extensive coral reefs located in zones of maximum hazard impacts underline not only the resilience of corals to tephra exposure but also show that volcanic materials provide substrates suitable for reef development. As fine scale estimation of coral reef biodiversity throughout the entire CT region is not available, the maps of species richness per ecoregion provided by Veron et al. (2009, Fig. 3) suit as the best available reference for coral diversity at regional scale. The identified areas of maximum hazard exposition do not particularly concur with patterns of maximum coral reef biodiversity. From

the presented results no conclusion can be made whether volcanic activities and the resultant hazards do either promote or suppress coral reef biodiversity in the CT. While tephra fall hazards in New Britain, North Sulawesi, and the Central Philippines are located in ecoregions of high coral diversity, the Bird's Head Peninsula of Indonesian Papua, where the maximum global biodiversity of zooxanthellate corals is found, is not at all affected by any hazard intensity to potentially shape species composition by disturbance impacts. Similarly, the species-rich coral reefs of Central and South Sulawesi are located outside the potential range of volcanic hazards (Fig. 5.3). Thus, despite the potential of tephra fall to locally eliminate coral reefs, other factors are at play to determine biogeographical patterns in coral reef ecosystems in the CT region.

5.4.4. Conclusion of tephra modelling in the Coral Triangle

Volcanic hazards from tephra deposition affect coral reefs by direct physical impairment and adverse habitat conditions. Reductions in live coral cover occur within few centimetres to decimetres of material accumulation and affect diverse species and various reef functional groups. At highest depositional rates, coral reefs may locally be destroyed but coral reef ecosystems are typically not eliminated over larger spatial scales. This can be accounted to the observed patchiness in hazard patterns. Original habitat heterogeneity, underwater relief, and wave exposure can mitigate disturbance impacts while coral colony regrowth may occur rapidly under suitable environmental conditions at habitat scale. Thus, there is great variance detected in the observed ecological reef response to tephra deposition.

Over temporal and spatial scales, the probability of high tephra loads on coral reefs in the CT is low and spatial association between tephra fall hazards and coral reef biogeography remains unclear.

6. Chapter 6 – Conclusion and future perspective

The case studies presented here show that volcanic activities have the potential to destroy coral reefs at a local scale. However, most severe effects are constrained in spatial extent or mitigated by habitat characteristics such as underwater topography and wave exposure. Abundant coral reef communities at volcanically affected locations and even in volcanic hotspots around the globe indicate recovery abilities of coral reef organisms. Times needed from ecosystem recovery vary greatly from months to millennia reflecting differences in hazard type and intensity as well as ecological reef state, individual species resilience, local biogeography, and potential additional stressors. Findings indicate that coral reef recovery after volcanic disturbances confirm the assumption of successional development characterized by species turnover and maximum diversity at intermediate disturbance frequency and intensity. Looking at the effects that volcanic activities impose on coral reef biodiversity and distribution reveals that active volcanism can be beneficial to coral reef communities resulting in elevated species numbers and enhanced coral reef distribution. Volcanoes are a major driver of coral reef formation around the globe by generating shallow-water habitats suitable for coral colonization and thus reef formation.

As tephra fallout from explosive volcanic eruptions has the potential to affect coral reefs even over larger spatial scales, tephra fall hazards to coral reefs were simulated by probabilistic modelling in the CT. Consulting scientific records allowed for definition of critical threshold values of tephra fall intensities on coral reef organisms. It can be concluded that even the lightest hazards from tephra deposition affect coral reefs. According to species-specific resilience impact severity rises with increasing hazard intensity. At isopach levels of 30 cm at minimum entire coral reef communities might be lost. Projecting those findings to the model results indicates that over temporal and spatial scales probabilities of such fatal tephra loads onto coral reefs in the CT are low. However, the results show that a significant proportion of regional coral reefs is likely affected by volcanic hazards from tephra fall at lighter intensities.

As a potential spatial association between tephra fall hazards and coral reef biogeography remains unclear, this would be a good starting point for further research. This study indicates that tephra fall does not exclude coral reefs over large spatial scales but how do volcanic disturbances from tephra deposition relate to coral reef biodiversity? Future work to estimate hazard exposure to coral reefs at a regional level depends on reliable and coherent spatial

long-term data on ecological characteristics, such as biodiversity to enable identification of causalities between natural disturbances and ecological coral reef responses. Future hazards assessment will greatly benefit from detailed spatial data sources, like high-resolution maps of global coral reef biodiversity as presented in the Allen Coral Atlas (Allen Coral Atlas 2020), to be linked to hazard maps.

Special scientific attention should be given to coral reefs that will be impacted by volcanic perturbations in the future. More detailed of an ecological archive with pre- and post-eruption data on the coral reef state, the fate of individual species and specimens time logged with changes of the environmental conditions at habitat scale would be an advantage. Such baseline information is essential to evaluate the role of volcanic activities in the future disturbance regime to coral reefs und climate change conditions. Selection of volcanically-affected coral reef sites in the CT could be based on the hazard maps presented in this study.

7. References

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8. Appendix

Table A1: Data resources used for probabilistic assessment of tephra deposition in the Coral Triangle.

Data	Description	Publication	Source	Access date
CTI-CFF Implementation Area	Coral Triangle Initiative implementation zone	Coral Triangle Initiative on Coral Reefs, Fisheries and Food Security 2009	http://ctatlas.coraltriangleinitiative.org/Dataset	03.09.2021
Exclusive Economic Zones	Spatial representations of Exclusive Economic Zones	Flanders Marine Institute 2019	https://www.marinerregions.org/downloads.php	03.09.2021
Holocene volcanoes	Holocene active volcanoes	Siebert and Simkin 2002	https://volcano.si.edu/list_volcano_holocene.cfm	03.09.2021
Holocene eruptions	Holocene volcanic eruptions per country from Burma (Myanmar), China, Fiji, India, Indonesia, Japan, Papua New Guinea, Philippines, Solomon Islands, Taiwan, United States, Vanuatu, Vietnam	Siebert and Simkin 2002	https://volcano.si.edu/search_eruption.cfm	07.09.2021
Wind	Atmospheric pressure over 37 altitudinal levels was retrieved from the ERA5 data set	Hersbach et al. 2020	https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-pressure-levels?tab=overview	09.09.2021
Coral distribution	reef Global distribution of shallow-water tropical and subtropical coral reefs	UNEP-WCMC et al. 2010	https://data.unep-wcmc.org/datasets/1	
Coral biodiversity	reef Estimates of global zooxanthellate biodiversity per biogeographic ecoregion	Veron et al. 2009		
Geographic ranges of reef corals in the Indo-Pacific	Geographic distribution outlined by range boundaries of individual reef coral (Scleractinia) species	Hughes, Connolly, and Keith 2013		
Land surfaces	Vector data provided by Natural Earth		https://www.natural-earthdata.com/	