Linking in-situ and remote sensing data for a better understanding of ecological changes in forest ecosystems of La Palma, Spain

DISSERTATION

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Frank Weiser

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Prüfungsausschuss:

Prof. Dr. Carl Beierkuhnlein (Gutachter)
Prof. Dr. Manuel Steinbauer (Gutachter)
Prof. Dr. Cyrus Samimi (Vorsitz)
Prof. Dr. Thomas Köllner

Dedicated to Ida and Alva

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Dissertation Summary

German Summary

Biodiversität wird auf verschiedenen räumlichen und zeitlichen Ebenen von einer Vielzahl an komplexen Prozessen und Umweltgradienten beeinflusst. Ein wichtiger Einfluss, das Störungsregime, kann als Filter während der Evolution von Arten agieren, aber auch kurzfristige Änderungen der Artenzusammensetzung von Ökosystemen auslösen. Ein anderer, die Ankunft neuer Arten, kann die Artenvielfalt erhöhen, doch auch die bestehende Diversität negativ beeinflussen. In den letzten Jahrzehnten haben sich das Störungsregime und Invasionsprozesse durch den Klimawandel und anthropogene Einflüsse rapide verändert. Umso wichtiger ist es, die Auswirkungen beider Prozesse auf lokale Artenvielfalt zu dokumentieren und zu verstehen. Die in den letzten Jahren steigende Verfügbarkeit von Fernerkundungsdaten bietet viele Möglichkeiten, in situ Daten mit Satellitenbildern zu kombinieren und gemeinsam zu analysieren, die Beobachtungsfrequenz zu erhöhen, bestehende Muster besser zu verstehen und die Herausforderungen einer sich ändernden Welt zu meistern.

Inseln sind Zentren der Artenvielfalt und beherbergen eine überdurchschnittliche Anzahl endemischer Arten, obwohl die Gesamtzahl der Arten niedriger ist als auf dem Festland. Die Inselbiogeografie untersucht sowohl Muster in der aktuellen Verteilung der Arten als auch deren Evolution über Millionen von Jahren. Inseln werden häufig als „Natural Laboratories“ bezeichnet, da sie es erlauben, vielfältige Umweltgradienten, z.B. Isolation, Topographie, Inselalter oder Inselhöhe und deren Auswirkung auf Artbildung und Artenzusammensetzung zu untersuchen. Die Inselbiogeografie erlaubt hierbei die Untersuchung von Prozessen, die sonst häufig durch andere Faktoren überlagert sind. Zusätzlich gerät die Biodiversität auf Inseln in den letzten Dekaden zunehmend unter Druck durch den Klimawandel, Invasionsprozesse oder anthropogene Einflüsse wie etwa Landnutzungsänderungen.

Ein Faktor, der in der Inselbiogeografie oft nicht gebührend beachtet wird, ist die Rolle vom Störungsregime und Störungen, die von großräumigen Ereignissen, die ganze Inseln praktisch sterilisieren (z.B. Hurrikane oder Vulkanausbrüche) zu kleinen, häufigen, lokalen Ereignissen reichen. Diese Vorkommnisse stehen in Verbindung mit der Evolution endemischer Arten und deren Eigenschaften, z.B. Verholzung oder Feueranpassungen. Dazu beeinflussen Störungen Artengemeinschaften und ändern deren Artenzusammensetzung.

Die Manuskripte in dieser Doktorarbeit untersuchen die Effekte von Störungen auf die Wälder von La Palma. Das Studienobjekt der meisten Manuskripte, der Kanarenkiefernwald, hat sich unter dem Einfluss von Vulkanausbrüchen und Waldbränden entwickelt. Die namensgebende Kanarenkiefer, *Pinus canariensis*, kann selbst intensive Feuer überleben und sich von durch Vulkanausbrüche ausgelösten Schäden erholen. Ich untersuche die Auswirkungen eines Waldbrandes auf die α- und β-Diversitätsmuster der normalerweise eher artenarmen Pflanzengemeinschaften im Unterwuchs dieser Wälder. Zwei andere Manuskripte untersuchen, wie *P. canariensis* auf den Vulkanausbruch des Tajogaite im Jahr 2021 reagiert hat, welcher die umliegenden Wälder mit großen Mengen von Schwefelgasen vergiftete und mit einer bis zu mehreren Metern dicken Ascheschicht bedeckte. Ein Manuskript untersucht räumliche Schadensmuster im Kronendach, während ein weiteres Manuskript den Schwefel-, Stickstoff- und Kohlenstoffgehalt von Nadelproben untersucht und mit den Kronenschäden in Verbindung setzt.

Das zweite Ziel dieser Dissertation ist es, Synergien zwischen Fernerkundung und Feldmethoden zu erproben. Die Nutzung von Fernerkundungsmethoden steigt im letzten

Jahrzehnt rapide, vor allem durch die zunehmende Verfügbarkeit frei verfügbarer Daten und technischer Fortschritte, etwa verbesserten, günstigeren Drohnen oder frei verfügbaren hyperspektralen oder Lidar Daten. In der Inselbiogeografie ist die Fernerkundung noch nicht so weit verbreitet wie in anderen Bereichen, unter anderem weil hohe, gebirgige Inseln häufig bei Fernerkundungsanalysen ähnliche Probleme bereiten, wie Gebirge auf dem Festland (z.B. aufwendigere Vorprozessierung durch Schatten an steilen Hängen). Trotzdem ist die Fernerkundung gerade durch die häufige Abgelegenheit und Isolation von Inseln sehr nützlich. Zwei der Manuskripte verbinden Fernerkundung mit Felddaten. Das letzte Manuskript dieser Arbeit nutzt Bodendaten und Fernerkundungsdaten um die momentane Ausbreitung einer invasiven Art, die droht, Teile des Lorbeerwaldes auf La Palma zu verdrängen, zu kartieren und verknüpft dann das Ergebnis mit Modellierungsmethoden, um die zukünftige Nische der Art zu modellieren.

Das Ziel dieser Dissertation ist somit zweigeteilt: Ich trage einerseits zum besseren Verständnis der Effekte von Störungen auf den Kanarenkiefernwald La Palmas bei. Zusätzlich untersuche ich die Vorteile, die eine kombinierte Nutzung von Fernerkundungsmethoden und Feldmethoden für die Inselbiogeografie birgt.

English Summary

Biodiversity is shaped and influenced by a complex multitude of processes and environmental gradients on different spatial and temporal scales. One influence, the disturbance regime, acts as a filter during the evolution of species, but also causes short term changes of the species composition of ecosystems. Another, the arrival of novel species, can increase diversity but also threaten existing diversity. In recent decades, both the disturbance regime and invasion processes have been rapidly altered due to climate change and anthropogenic influence. It is therefore even more important to keep track of and understand the effect of these processes on local biodiversity. The recent rise in availability of remote sensing data offers many opportunities for combined analytic approaches using in situ data jointly with satellite images to significantly increase the frequency of observations, to aid in better understanding existing patterns and face challenges of a changing world.

Islands are hotspots of biodiversity and harbour a disproportionate number of endemic species while the overall number of species richness is generally lower compared to the mainland. Island biogeography investigates patterns in the distribution of these species and how this extraordinary richness evolved over millions of years. Islands are seen as perfect “natural laboratories” as they allow studying a multitude of environmental gradients and their effects on both speciation and community assembly, such as isolation, topography, island age or height. Island biogeography therefore allows insights into processes that are otherwise overlayed by other factors. In addition, in recent decades, the biodiversity of islands has come under threat due to climate change, invasion or anthropogenic influence such as land use change.

One factor often not paid due attention in island biogeography is the role of disturbances and the disturbance regime, which can range from large events effectively sterilizing islands (e.g. hurricanes or volcanic eruptions) to small, recurring, local events. These events have been linked to the evolution of endemic species and their traits, e.g. insular woodiness or fire adaptations. Additionally, disturbances affect current species communities and change their composition.

The manuscripts in this thesis investigate the effects of these events on the forests of La Palma. The study subject of most manuscripts in this thesis, the Canary Pine forests, has evolved under the influence of volcanic eruptions and fires. The name-giving species, *Pinus canariensis*, is well adapted to survive even severe fires and can recover from significant damage caused by volcanic eruptions. I investigate the effects of one of the frequently occurring wildfires on α- and β-diversity patterns of the generally species poor plant communities of the understory of one of these forests. Two other manuscripts investigate how *P. canariensis* reacted to the 2021 Tajogaite volcanic eruption, which poisoned the surrounding forests with large quantities of sulphur gases and covered them in a thick tephra layer. One manuscript detects spatial patterns of damage the canopy suffered while another manuscript explores needle sulphur, nitrogen and carbon content and how they link to the observed canopy damage.

The second focus of this thesis is to explore synergies between remote sensing and field data. The usage of remote sensing has strongly increased in the last decade, mainly due to the increasing wealth of openly available datasets and new technological advancements, such as improved, cheaper unmanned aerial vehicles or freely available hyperspectral or lidar data. Alas, remote sensing is still underused in island biogeography, in parts because high elevation islands pose similar difficulties for remote sensing analysis as mountain ranges (e.g. steep slopes make more pre-processing necessary). Nonetheless, especially the remoteness of many islands and the extreme isolation of many habitats makes remote sensing highly useful for island biogeography. Two of the manuscripts presented here combine remote sensing data with data sampled on the ground. The final study on this thesis uses ground truth data combined with remote sensing data to map the current extent of an invasive species threatening the laurel forest on La Palma and then further combines the results with modelling to map the future niche of this invasive species.

The aim of this thesis is therefore twofold: I aim to contribute to a better understanding of the effects of disturbances on the Canary Pine forests of La Palma. In addition, I explore benefits of combining remote sensing approaches with more traditional fieldwork methods to offer new possibilities for island biogeography.

1 Introduction

1.1 Motivation

1.1.1 Personal motivation

At the time of completion of this thesis, I have been on the island of La Palma three times, working in and visiting nearly all parts of the island. However, while La Palma is home to a remarkable diversity of unique ecosystems and species, one aspect fascinated me most: The incredible plasticity and resilience of the Canary Pine, *Pinus canariensis* C.Sm. and the respective implications for ecosystem dynamics. This species appears across a broad range of climatic conditions on the Canary Islands, ranging from arid environments with less than 300 mm of annual rainfall to moist environments with more than 1500 mm annual rainfall as they are found in the north-eastern part of the island. It can thrive from close to the sea level up to the alpine zone, reaching 2300 meters above sea level. It is closely linked to the water budget of the island, with trade wind clouds condensing and precipitating from its long needles. The monodominant stands of this endemic pine are effectively harvesting water from the passing clouds, which is of crucial importance for freshwater supply and economy. Additionally, Canary Pine colonizes young volcanic soils, and thus initiates ecosystem development after volcanic eruptions.

But even more fascinating than this broad range of conditions the species can thrive in are the outstanding adaptations to severe impacts of disturbances. During the field work for the manuscripts in this thesis, I saw individuals of *P. canariensi*s scorched by fire, damaged by volcanic bombs which ripped their branches off, poisoned by sulphuric gases and standing in lava flows. All these trees were alive and resprouting, and while the long-term survival and recovery of some of these individuals might be doubtful, most damaged trees appear to be able to survive even severe disturbances (Figure 1). During our fieldwork for Manuscript 1 presented in this thesis, me and my colleagues hadn’t encountered a single dead tree in a forest affected by one of the worst wildfires in recent decades. In addition, *P. canariensis* has been affected by volcanic eruptions for millions of years, evolving under their influence. As volcanic eruptions on the Canary Islands are rare on human timescales, these fundamental impacts have been widely ignored until today. While the 2021 Tajogaite eruption bestowed many hardships on the inhabitants on La Palma, it offered the unique opportunity, to directly monitor and investigate the effects volcanic eruptions have on these trees. I am glad to be able to contribute with my manuscripts to a better understanding of this extraordinary resilience and the effects disturbances have in Canary Pine forests.

Figure 1 Top: Canary Pine forest covered in tephra by the 2021 Tajogaite eruption with the needles showing chlorotic damage from volcanic gases. The same forest had burned in 2016. The trees are resprouting strongly in this picture taken in April 2022 and are already on their way to recovery.

Bottom: Resprouting buds in the bark and branches of an individual tree (both Photographs: Frank Weiser)

1.1.2 Scientific motivation

Climate change, globalization and land use change put increasing pressure on nature, leading to a serious decline in the state of nature, threatening biodiversity globally and causing the currently ongoing sixth mass extinction (Ceballos et al., 2015; Díaz et al., 2019). Islands are comparatively more affected than mainland ecosystems (Courchamp et al., 2014; Harter et al., 2015). This is especially troubling, because oceanic islands harbour a high number of endemic species which are especially vulnerable to changing conditions (Fordham & Brooks, 2010; Manes et al., 2021).

The outstanding richness of endemic species on oceanic islands and its reasons have been investigated since the times of prominent figures such as Charles Darwin or Alfred Russel Wallace (Darwin, 1859; Wallace, 1902). After the seminal "Theory of Island Biogeography" by MacArthur and Wilson (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967) generations of scientists have investigated biodiversity patterns on islands. Islands have been called "Natures laboratories" (Whittaker et al., 2017) and this research arena is still intensely studied to understand fundamental patterns of biodiversity and speciation.

Disturbances play an important role for island biodiversity on various spatial and temporal scales yet are not given enough importance in biogeographical theories investigating island biodiversity (Whittaker & Fernández-Palacios, 2007). Some disturbances, e.g., those associated with volcanism, are an inherent part of the life cycle of oceanic islands and therefore play a crucial role for the geodiversity and topography of oceanic islands, which directly affects the species richness of islands (Gillespie & Roderick, 2014; Irl et al., 2015; Bailey et al., 2017). Disturbances also act as an evolutionary pressure during selection and speciation and therefore are linked with traits that develop on islands, e.g., the extraordinary fire resistance of *P. canariensis*, the subject of some of the manuscripts in this dissertation, or more recently, as an explanation for insular woodiness (Beierkuhnlein et al., 2023). Disturbances may also drive species to extinction. Island endemics are especially vulnerable to this due to their small population sizes and slow responses to changing environmental conditions (Manes et al., 2021). This risk will grow with climate change due to the expected increase in extreme events with climate change and then further contribute to the disproportionally high extinction rate of island endemics.

The island of La Palma is well suited to study the effects of disturbances on biodiversity. It is comparatively young with 1.7 Ma. Islands usually reach their peak of species richness at 2.5 Ma of age but the peak of endemic species richness is usually reached at around 10 Ma of age (Steinbauer et al., 2013). La Palma therefore offers the opportunity to investigate many disturbances shaping local biodiversity in action. The goal of this thesis is to investigate several effects of disturbances on the *P. canariensis* forests of La Palma. The endemic *P. canariensis* has been present on the Canary Islands for 13 million years and is therefore adapted well to volcanic eruptions and subsequently to fire.

Fires have become frequent in these forests since the arrival of humans on the archipelago, and they not only affect *P. canariensis* but also the understory vegetation of forest ecosystems (Molina-Terrén et al., 2016). However, the spectrum of diversity measures has not been applied to this ecosystem before. This is why **Manuscript 1** is focused on the effects of fire on α- and β-diversity.

While La Palma is shaped by frequent volcanism with seven eruptions in the last 500 years, eruptions are rare on human timescales. The recent Tajogaite eruption offered the unique opportunity to directly investigate how *P. canariensis* reacts to sulphur emissions in **Manuscript 2** and was the first eruption on La Palma, where remote sensing data was broadly available to analyse the impact.

In **Manuscript 3,** I explore the direct effects of sulphur gases and tephra deposits on the needle composition of *P. canariensis* by analysing their nitrogen, carbon and sulphur content after the end of the 2021 eruption. In addition, the needle data is combined with remote sensing images at different timesteps to test correlations between needle properties on the ground and visible canopy damage in satellite imagery.

The general approach of this dissertation is linking the two main approaches in Earth Observation, the implementation of remote sensing methods together with in-situ data. The amount and quality of freely available remote sensing data has been increasing explosively in recent years, with more and more different sensors becoming available. Exploiting remote sensing data offers many unique opportunities for island biogeography. For example, it allows frequent monitoring of even the most isolated islands and habitats and can reveal patterns that would otherwise be hidden or hard to detect from the ground.

Some of the weaknesses of remote sensing, such as the spatial resolution or a certain bias while interpreting the data can be alleviated by supporting remote sensing data with field work data. This combined application of field and remote sensing data is currently underused in island biogeography. While **Manuscript 2** is purely remote sensing based, **Manuscript 1, 3** and **4** make use of both freely available satellite images and ground data gathered in the field. **Manuscript 4** uses satellite data and ground truth to investigate how *Castanea sativa* Mill. invades the laurel forests of the island La Palma and models future possible distributions of the invasive tree species on the island, further showing the power of combined analytic approaches in island biogeography.

To summarize, this thesis aims at to contributing to the understanding how disturbances affect the well adapted forest ecosystems on the island of La Palma while using both remote sensing and field work and exploring the power and synergies of complimenting in situ data with remote sensing imagery and analysis.

Table 1 Short summary of the Manuscripts (MS) presented in this thesis and their main findings

MS	**Title**	**Contribution**	**Disturbance**	**Major findings**
1	Impacts of Forest Fire on Understory Species Diversity in Canary Pine Ecosystems on the Island of La Palma	First author	Fire	- Elevation is the most important driver of understory α- and β-diversity in Canary Pine forests after fire - Other environmental factors and fire intensity were only of minor importance - *Lotus campylocladus* ssp. *hillebrandii* has a strong influence on understory species richness after fire, with sites covered by the species showing otherwise significantly lower species richness
2	Impact of Volcanic Sulfur Emissions on the Pine Forest of La Palma, Spain	First author	Volcanic sulphur emissions	- Chlorotic damage suffered by *Pinus canariensis* closely linked to distance from the eruption - Wind direction only played a minor role for detected canopy damage - Canopy damage was visible up to 7 km from eruption
3	Combining in-situ monitoring and remote sensing to detect spatial patterns of volcanic sulphur impact on pine needles	First author	Volcanic sulphur emissions and tephra deposition	- Sulphur and carbon levels of sampled *P. canariensis* needles showed a distance-based pattern similar to damage detected in Manuscript 2 - Distance was the most important predictor for needle sulphur levels - Needle sulphur was the most important predictor for needle nitrogen and carbon levels - Needle contents were not correlated with canopy damage detected with remote sensing
4	Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island	Supervision of underlying master thesis and co-author	Invasive species	- The combination of field presence data and remote sensing methods (supervised classification) is well suited to map the present distribution of the invasive *Castanea sativa* on La Palma - Species distribution models synergize well with the results to predict future habitat suitability of the species - *C. sativa* currently occupies 1.2% of the island, with 12-17% being climatically suitable habitats

1.2 Structure of this thesis

In the beginning of the introduction, I describe the role of islands as hotspots of global biodiversity. I present the status quo as well as the mechanisms leading to the extraordinary endemic species richness of oceanic islands. Then I draw attention to current and future threats to insular biodiversity. Next, the role of disturbances in shaping past, current and future biodiversity on islands will be pointed out. The disturbance regime is underrepresented in many biogeographical theories relating to islands yet is an important factor.

In the second part of the introduction, I will lay out patterns of biodiversity and the disturbance regime of my study area, the island of La Palma. The study subject of three of the four manuscripts in this thesis, *Pinus canariensis*, is introduced with its past and present distribution and the reasons for its limits. Additionally, the extraordinary resilience of the species to different disturbances, such as fire or volcanic eruptions, is explained.

The role of remote sensing, a field which has steadily increased in importance in recent years, in island biogeography is summarized. Compared to more traditional methods such as floristic work or field data gathering, remote sensing offers datasets with a so far unseen temporal resolution and many novel possibilities. All manuscripts in this thesis use remote sensing methods alone or combined with field data to investigate patterns of α- and β-diversity or disturbance effects on the local flora.

In the synopsis I present the manuscripts included in this thesis. I summarize how each manuscript investigates the role of a specific disturbance for the diversity on La Palma. I also explain the novel contribution of each manuscript to the understanding of local species diversity on the island. The synopsis is concluded by identified research gaps.

Then, my manuscripts and my contribution to each manuscript follow. Finally, this dissertation ends with the Appendix, in which all scientific presentations given during the creation of this thesis as well as other manuscripts not included in this thesis are listed.

1.3 The outstanding contribution of islands to global biodiversity

1.3.1 Theories and concepts on island biodiversity

The distribution of species is not random, but rather shaped and influenced by a multitude of gradients and environmental drivers (Whittaker, 1967; Austin, 1987; Rosenzweig, 1995). Many of these gradients exhibit high variability even on small scales (Palmer & Dixon, 1990; Dewar & Richards, 2007). Gradients also often overlap (Pausas & Austin, 2001; Slaton, 2015), with species richness often being determined by at least two gradients at the same time (Margueles, 1987; Pausas, 1994; Austin et al., 1996; Pausas & Austin, 2001). The isolated nature of islands offers the opportunity to study the effect of environmental drivers on species diversity and community assembly (Gillespie, 2004; Whittaker & Fernández-Palacios, 2007; Emerson & Gillespie, 2008). Additionally, there are various physical island types with different environmental conditions (Ali, 2017). Islands are therefore often seen as "natural laboratories" to test theories and hypotheses.

Before this multitude of gradients and environmental conditions of islands can influence species, species first have to arrive on an island. How immigration of species and subsequent extinction once the island fills up with species result in a stable state with a certain number of species has been summarized in the seminal "Equilibrium model of island biogeography", by MacArthur and Wilson (MacArthur & Wilson, 1963; MacArthur & Wilson, 1967; MacArthur, 1972). It predicts an equilibrium in the number of species, which is positively influenced by island size and negatively influenced by distance to the continent, based on the immigration and extinction rate. Several early studies support this theory (e.g. Simberloff & Wilson, 1969, 1970), which have been reviewed in Simberloff (1974). Other studies point out flaws in the supporting studies (McGuiness, 1984), especially their use of the power function behind it (Connor & McCoy, 1979), lack of proper testing of the hypothesis (Simberloff, 1976) or a lack of testing of other models (Coleman et al., 1982). A review of early criticism of the theory can be found in Gilbert (1980). In more recent years, the equilibrium theory of island biogeography is still seen as controversial. On the one hand, its simplicity is seen as problematic, making new models necessary to capture our increased understanding of complex links and relationships responsible for species diversity (Brown & Lomolino, 2000; Lomolino, 2000; Kalmar & Currie, 2006; Heaney, 2007). It also does not apply well on evolutionary timescales, because it does not adequately represent phylogenesis (Heaney, 2000) or island age (Carlquist, 1974; Borges & Brown, 1999). Islands reaching an equilibrium is also considered as unlikely, because too many external factors e.g. geological and climatic changes can outpace colonization (and speciation, which is a part of other equilibrium models) (Heaney, 1986).

On the other hand, the theory is still seen as a useful framework to investigate island species richness (Heaney, 2000) and can be used as a basis for more complex models such as the species-energy theory (Wright, 1983), the general dynamic theory of island biogeography which includes time as a dimension (Whittaker et al., 2008) or models incorporating speciation together with immigration and extinction (Chen & He, 2009; Rosindell & Phillimore, 2011). Some of the general patterns the theory predicts are also well observed: More isolated islands generally have lower species numbers due to the rarity of colonization, even at evolutionary timescales (Weigelt et al., 2013). Area is the most important predictor for species richness of islands (Kreft et al., 2008), but while this relationship has been observed for a long time (Forster, 1777; Forster, 1778) the form of this species-area relationship is still under debate (Rosenzweig, 1995; Lomolino, 2001; Lomolino & Weiser, 2001; Dengler, 2009; Triantis et al., 2012). Suspected reasons for large islands harbouring more species include a higher resource availability, higher habitat diversity and speciation potential, respectively (Kreft et al., 2008).

A big part of the diversity on islands is attributed to "explosive radiation events" (Fernández-Palacios et al., 2021a), where colonizing species from a broad range of taxa evolve, filling available niches in heterogeneous but as-of-yet species poor island environments (Schluter, 2000; Losos & Ricklefs, 2009; Losos & Mahler, 2010). This process known as adaptive radiation goes back to the work of Charles Darwin and Alfred Russel Wallace (Darwin, 1845; Darwin, 1859; Wallace, 1902). Ecological opportunity, meaning e.g. an available niche (in the Grinnellian sense (Grinnell, 1917)) to fill, has been defined as a prerequisite for adaptive radiation (Stroud & Losos, 2016; Gillespie et al., 2020) but there are contrasting viewpoints (Losos, 2010). While some clades radiate, others don't (Losos & Mahler, 2010). Speciation can also happen without ecological divergence and little to no niche differentiation as "nonadaptive radiation" (Gittenberger, 1991; Czekanski-Moir & Rundell, 2019) with initial evidence going back nearly as far as Darwin's and Wallace's work (Gulick, 1872). Nonadaptive radiation often results in allopatric or parapatric taxa (Rundell & Price, 2009) but can also happen in sympatric taxa (Xu & Shaw, 2020). The speciation rate can be modified along environmental gradients. Coupled with open Grinnellian niche space gradients can offer both drivers and opportunity for speciation (Wiens & Graham, 2005; Schluter & Pennell, 2017).

1.3.2 Current trends in island biodiversity

Oceanic islands are hotspots of global biodiversity. Nine out of 25 global biodiversity hotspots are made up by islands and virtually all tropical islands fall into a biodiversity hotspot (Myers et al., 2000). While islands only account for 3.5% (Whittaker et al., 2017), 5.3% (Tershy et al., 2015) to 7.9% (Sayre et al., 2019) of terrestrial surface area, depending on definition, they host 19% of bird species, 17% of rodents and 17% of plants (Tershy et al., 2015) or, more generally described, 15-20% of terrestrial species (Whittaker et al., 2017). Islands are not equally distributed around the globe. 65% of islands are tropical with wet temperate climates prevalent (Weigelt et al., 2013). The number of islands strongly depends on definition of size: There are an estimated 370.000 "islets" above 0.01 km² and approximately 20.000 islands >1 km² (Weigelt et al., 2013). The latter is arguably a good threshold for minimum island size in ecological studies, as stochastic events are the most important drivers of diversity on smaller islands (Lomolino & Weiser, 2001), while both speciation and endemism are rare at these sizes (Losos & Schluter, 2000; Kisel & Barraclough, 2010).

The overall number of species on islands is generally lower compared to the mainland, but they are characterized by a high proportion of endemic species, hosting about one quarter of endemic plants (Kreft et al., 2008; Kier et al., 2009). Additionally, even comparatively small archipelagos can host an astonishing number of endemic species, with e.g. New Caledonia being home to the same number of endemic species as all of Europe (Petit & Prudent, 2008). Due to a lack of contact to the mainland, most of their endemic species have evolved in situ out of colonizing species as described above (Whittaker&Fernández-Palacios, 2007). Higher habitat diversity of islands also leads to higher species richness (Hortal et al., 2009), signifying in turn that endemic species often only occur in specific, and spatially limited habitats (Kruckeberg & Rabinowitz, 1985).

1.3.3 Threats to biodiversity

1.3.3.1 General threats to biodiversity

The outstanding biodiversity of islands is under pressure from a multitude of factors (Cajaupe-Castells et al., 2010; Harter et al., 2015; Ripple et al., 2017; Díaz et al., 2019; Veron et al., 2019). Islands harbour ~50% of currently threatened species while 75% of extinction events occurred on islands (Fernández-Palacios et al., 2021b) as well as 90% of bird species extinctions in the last

400 years (Petit & Prudent, 2008) due to several reasons (Gray, 2019). Island species are disproportionately threatened compared to continental species, with 60% of documented extinctions in the last 500 years being island endemics (Whittaker et al., 2017). Threats to island biodiversity will therefore strongly influence the fate of global biodiversity (Simberloff, 2000). A big part of this threat is caused by humans, with e.g. vegetation turnover increasing sixfold after human arrival on islands (Nogué et al., 2021). Many extinction events caused by early settlers are well documented, e.g. the Moa on New Zealand (Holdaway et al., 2000) or the Dodo on Mauritius (Roberts & Solow, 2003). Along with those events, where humans are the direct cause for a species to go extinct, the indirect effects can be catastrophic as well. Habitat loss and invasion have negatively affected islands for centuries, while climate change and the linked sea level rise are increasing in importance in the last decades (Russel & Kueffer, 2019), with even a moderate sea level rise significantly threatening biodiversity hotspots and their endemic species (Bellard et al., 2014).

1.3.3.2 Invasion as a threat to island biodiversity

Invasion contributes significantly to the pressure on island biota (Bellard et al., 2017; Leclerc et al., 2018; Lenzner et al., 2020), changes local ecosystems and contributes to the extinction of native species (Bellard et al., 2016; Pyšek et al., 2020). Islands are hotspots of invasion and are more threatened by negative effects of invasion compared to the mainland (Simberloff, 1995; Dawson et al., 2017; Gray, 2019) although some archipelagos prove unusually resistant to invasion (Fernández-Palacios et al., 2023). Invading species affect the local flora and fauna in numerous ways, e.g. by competing for resources (Gioria et al., 2014), introducing pathogens or altering the ecosystem (Fernández-Palacios et al., 2023).

How susceptible islands are for invasion varies strongly (Kueffer et al., 2010), with more isolated islands and islands with lower species numbers (Daehler, 2006; Moser et al., 2018) more prone to invasion. Differences in precipitation, human impact (Irl et al., 2021) or elevation (Alexander et al., 2011) further influence invasion patterns. Many invasive species become naturalized, with islands harbouring six times the amount of naturalized alien plant species and three times the number of invasive species compared to the mainland (Essl et al., 2019).

Additionally, endemic species usually are weak competitors, as the main problem for species is initially arriving on the islands and then coping with the environmental conditions, rather than many other species competing for the same resources. Human introduced species have comparably easy access to islands and can become invasive because of their ability to outcompete endemic and native species. Figure 2 shows *C. sativa,* the subject of **Manuscript 4**, which was introduced to La Palma and now threatens the laurel forest. In addition to invasive plants negatively affecting the local flora, introduced herbivores put pressure on endemic species, which have often evolved without defence mechanisms to herbivores due to their absence during their evolution (Courchamp et al., 2003).

Figure 2: Chestnut, *Castanea sativa* (brown patches, the species is the only tree on the island shedding its leaves in winter), in the Fayal-Brezal of La Palma. *C. sativa* was introduced on the island 500 years ago for agriculture, where it now invades the surrounding forests from abandoned orchards. The species threatens to replace parts of the laurel forest on the island. (Photograph: Frank Weiser)

Managing invasive species is seen as crucial for the protection and restoration of islands (Glen et al., 2013), especially considering that post-invasion management is 25 times as expensive as pre-invasion management (Cuthbert et al., 2022). This is, however, not an easy task, as globalization has led to a stark increase in species invasion across taxa (Ricciardi et al., 2021). Invasion rates are also still on the rise with a 36% increase expected in established alien species globally between 2005 and 2050 (Seebens et al., 2021) facilitated by a current lack of saturation with species (Seebens et al., 2017).

1.3.4 The role of the disturbance regime for island biodiversity

Disturbances and the disturbance regime have been investigated thoroughly (White & Jentsch, 2001), but are not paid due attention in island biogeography (Whittaker & Fernández-Palacios, 2007). The disturbance regime describes the sum of all disturbances acting on a landscape over a longer time period. Disturbances are often defined as “any relatively discrete event in time that removes organisms and opens up space which can be colonized by individuals of the same or different species" (Begon et al., 1990). Other, broader definitions understand disturbances as mechanisms removing biomass (Grime, 1977) or a "deviation" from (Odum et al., 1979) or "perturbation" of (Pickett & White, 1985) the normal state of an ecosystem. These definitions are problematic, however, as the "normal" state and the frequency of disturbances would need to be known and static parameters would have to be assumed. Therefore, disturbances should rather be defined as a "measurable, abrupt change of ecosystem variables" (Wohlgemuth et al., 2022).

The disturbance regime entails not only the sum of the single disturbances present, but also their interactions and coherences. These interactions are often counterintuitive or even surprising, e.g. individual events randomly co-occurring with other disturbances, promoting or inhibiting each other and even complex disturbance cascades (Burton et al., 2020). As an example, a recent study from Fogo Island revealed evidence for an increase on both fire frequency and erosion caused by increased volcanic activity (Castilla-Beltrán et al., 2023).

There is still a need for general, unifying theories in disturbance research (White & Jentsch, 2001; Jentsch & White, 2019). The most well-known theory on the effects of disturbance on species richness is the "Intermediate Disturbance Hypothesis" (further called IDH) (Connell, 1978). It postulates, that disturbances allow establishment of early succession stage species in late-stage environments. However, too frequent or too intense disturbances force out late-stage species completely. The highest diversity can therefore be found at moderate disturbance rates and intensities, displaying a hump-shaped relationship. While empirical evidence for the hypothesis is lacking (Mackey & Currie, 2001; Randall-Hughes et al., 2007) and the theoretical background has been strongly criticized (Fox, 2013), the IDH is a useful concept that can be tested and critically applied (Sheil & Burslem, 2003; Sheil & Burslem, 2013).

To understand species turnover patterns on islands, it is essential to consider disturbances, as they can significantly alter the habitability and resource availability of island systems and in general cause a wide array of biotic responses and changes (Delcourt & Delcourt, 1988, 1991) Disturbances on islands reach from small scale, local events to large scale events, that can in theory even sterilize islands, at least to a degree, such as the eruption of Krakatau (Whittaker et al., 1989) or the Roque Nublo eruptive period, which pushed many species to extinction on Gran Canaria ~3.5 Ma ago (Emerson, 2003). Disturbances like volcanic eruptions can also directly influence speciation processes, as they are able to isolate populations (Gillespie & Roderick, 2014).

In island biogeography, the equilibrium theory of island biogeography does not take disturbances sufficiently into account (Whittaker, 1995). MacArthur & Wilson (1967) recognized that disturbances played a role but thought them of minor importance compared to their equilibrium model (Whittaker, 2000).

Disturbances can push islands to an "unattained equilibrium", where disturbances and other changing environmental conditions keep an equilibrium out of reach and outpace colonization and speciation (Heaney, 1986; Warren et al., 2015). How disturbances affect the stability of a system varies by disturbance type and affected species and communities (Radchuck et al., 2019) and the ratio between the duration of the disturbance effect and the recovery time (Turner et al., 1993).

For islands, the effects of disturbances have been summed up early as the "Disturbance Hypothesis" (Rutzler, 1965; Osman, 1977; Sousa, 1979; McGuinness, 1984), which postulates, that disturbance intensity and frequency decreases with island area, therefore leading to increased species diversity with increasing area. In a similar vein, the idea of a moving equilibrium between establishing species and species going extinct (which can be caused by disturbances) was also named "dynamic nonequilibrium hypothesis" (Whittaker, 2000) or "dynamic disequilibrium" (Heaney, 2000).

Nonetheless, non-equilibrium dynamics are still not well understood (Warren et al., 2015) and the role of the disturbance regime is often not integrated in many theories of island biogeography. Disturbances can also amplify each other or change environmental conditions, increasing the importance to pay more attention to them (Ross et al., 2009). And if disturbances are investigated, then rather as a single event, not as a recurring occurrence which affects biota to a similar degree as e.g. habitat diversity or changing climatic conditions.

1.3.5 Changing disturbance regime

Hand in hand with climate change, disturbance regimes are changing with increasing tempo, making understanding them and their effects all the more crucial (Turner, 2010). However, research on the changing disturbance regime on islands is still underrepresented compared to other systems, such as mainland forest systems, where more knowledge exists (e.g. Millar et al., 2007; Seidl et al., 2011; Seidl et al., 2017; Senf & Seidl, 2021) and is expanding (Lindner et al., 2014).

The disturbance regime is expected to be significantly altered by climate change for many regions, with drastic changes to circulation patterns (e.g. El Niño) and a stark increase in frequency and magnitude of many disturbances and extreme events (Dale et al., 2001; IPCC, 2023). Not only will extreme events increase in frequency, but they will likely also reach new intensities (Jentsch & Beierkuhnlein, 2008). This increase in disturbances will be particularly challenging for island biota for several reasons. Small islands can be completely affected by disturbances, e.g. hurricanes. In many cases, endemic species are spatially very restricted and highly specialised (Kruckeberg & Rabinowitz, 1985), leading to very small population sizes (Gillespie et al., 2008). Small population sizes also lead to lower genetic diversity of island inhabiting species, especially endemics, amplifying this vulnerability (Frankham, 1997; Frankham, 1998). This means, that if disturbances and environmental changes lead to the formation of new microhabitats or change existing ones, endemics often exhibit a reduced ability to adapt (Hermant et al., 2013).

Endemics are also characterized by a lack of dispersal ability (Lavergne et al., 2004). While this specialization on local persistence might be beneficial when occupying specific habitats, as the chance of distribution to other habitats such as other islands or the mainland are low given the isolation of islands, it decreases the chance of surviving populations when affected by disturbances. Both island size and habitat size make many endemic species therefore sensitive to an increase of stochastic events (Kruckeberg & Rabinowitz, 1985; Gilpin & Soule, 1986). Overall, biodiversity on islands is therefore disproportionally vulnerable to changes in the disturbance regime with climate change, further contributing to the high extinction rates and growing extinction debt of islands (Harter et al., 2015).

1.4 Biodiversity on La Palma

1.4.1 Current status

The Canary Islands and their unique flora and fauna rich in endemic species has been the subject of studies for centuries. The first botanical studies were published in 1799 (Viera y Clavijo, 2005) and illustrious natural scientist such as Humboldt and Darwin were fascinated by the flora of the archipelago (Humboldt & Bonpland, 1826; Darwin, 1839). In the 19th century, more attempts of comprehensive Canary Island Floras were made (Webb & Berthelot, 1844; Christ, 1885; Christ, 1887). These early works were followed by a wave of floristic works on vascular plant diversity on the archipelago (e.g. Erikson et al., 1974; Hohenester & Welss, 1993; Bramwell, 1997). For a more comprehensive overview, the recent FloCan Checklist summarizes and unifies the wealth of floras into one checklist (Beierkuhnlein et al., 2021).

Nonetheless, even with this substantial number of floristic assessments, evaluating the current state of vascular plant species diversity on La Palma is difficult due to both new discoveries and disappearances of existing species and changing taxonomies. Currently, La Palma harbours the relatively low number of 1161 vascular plant species, a high percentage (18%) of which are endemic. With its age of ~1.7 Ma, La Palma is still in the early stages within the life cycle of the Canarian archipelago, where islands typically reach 20 Ma of age before they disappear. However, it is close to the modelled peak of species richness, which is expected at 2.5 Ma and yet has to reach the maximum amount of single island endemics, which is expected at ~10 Ma (Steinbauer et al,. 2013a).

On La Palma, both steep topographic and climatic gradients lead to endemic richness (Irl et al., 2015). The climate on La Palma can be divided based on the trade winds, which continuously bring clouds to the north-eastern coast of La Palma but do not reach the much drier western, leeward part (del-Arco et al., 1999). Overall, precipitation conditions on the island range from humid to hyperarid (Garzón-Machado et al., 2014)

La Palma still is dominated by natural and semi-natural vegetation, with only one third of the island used for agriculture (Irl & Beierkuhnlein, 2011). The whole island has therefore been designated as an UNESCO Man and the Biosphere Reserve. High endemic diversity is observed in high elevation and rocky habitats (Fernández-Palacios et al., 2021a). On La Palma, the alpine zone is situated above a trade wind inversion (Fernández-Palacios, 1992; Fernández-Palacios & de Nicolás, 1995). This inversion shapes the alpine zone with its dry conditions, high temperature amplitude between day and night, high solar radiation and frequent ice and snow cover (Irl & Beierkuhnlein, 2011; Irl, 2014). High elevation habitats are ecologically more isolated as they are further away from comparable high-elevation sites on the mainland, explaining their remarkable speciation (Steinbauer & Beierkuhnlein, 2010; Steinbauer et al., 2013b) resulting in a high number of single island endemics (Steinbauer et al., 2012). The degree of isolation, however, changed in the past, with sea level changes during the Pleistocene significantly affecting single island endemic richness (Rijsdijk et al., 2014; Fernández-Palacios, 2016; Norder et al., 2019).

Other habitats with high species richness or endemic richness include Lapilli fields and lava flows, where richness increases with time (Irl et al., 2019; Eibes et al., 2021). The valleys of the north-eastern coast are home to the laurel forest, a relic from Paleo-Macaronesia (Höllermann, 1981; Fernández-Palacios et al., 2011). Another example with a high degree of endemism is phonolitic rocks on the Canary Islands, which are "islands within an island" due to their unique form and composition compared to their surroundings. They are characterized by higher species richness compared to the area around them and they host highly endemic species (Kienle et al., 2022). They are home to *Cheirolophus junonianus* (Svent.) Holub, a single island endemic with two varieties mostly restricted to one single phonolite each and only about 100 individuals left (Garnatje et al., 1998).

Like other islands worldwide, biodiversity on La Palma is threatened by a multitude of impacts, such as land use, changing precipitation patterns, invasion by herbivores, and invasive species. It has been estimated that the Canary Islands carry a considerable extinction debt, with a series of endemic species destined to become extinct even without further habitat loss (Otto et al., 2017). Not only species but also whole ecosystems are under pressure, like the laurel forest which is considered "vulnerable" on the Red List of European Habitats (Jannsen et al., 2016) and has been long affected by anthropogenic disturbances (Parada-Díaz et al., 2021). Characteristic vegetation units (e.g. thermo-sclerophyllous woodland) on the Canary Islands have drastically reduced in extent with little hope of recovery due to human land use (del Arco Aguilar et al., 2010; Castilla-Beltrán et al., 2021).

1.4.2 Disturbances and invasion on La Palma

1.4.2.1 Volcanism

La Palma is part of the Canary Island Seamount Province, a volcanic hotspot track on the African plate. This track is ~1300 km long, ~350 km wide and consists of more than 100 seamounts reaching up to 142 Ma in age (van den Bogaard, 2013). The mechanism behind this chain of volcanic seamounts is yet under debate (Carracedo et al., 1998) with studies supporting e.g. edge-driven convection (King & Ritsema, 2000), mantle plumes (Geldmacher et al., 2005; Carracedo et al., 2015; Zaczek et al., 2015) regional fractures or rifts (Anguita & Hernán, 1975; Anguita & Hernán, 2000; Geyer & Martí, 2010) as the driving force. In contrast to the well studied Hawaiian archipelago, the Canary Islands reach older ages of up to 23 Ma due to a lack of subsidence while Hawaiian Islands are eroded in a more tropical climate already after 7 Ma (Carracedo, 1999).

Volcanism and geology of La Palma are well studied (Carracedo et al., 1998). The Caldera de Taburiente on La Palma offers the unique opportunity to study the whole shield of the volcano visible and accessible, starting from the submarine base (Guillou et al., 2001). A multitude of studies therefore date, structure and stratify various parts of the island (e.g. Staudigel & Schmincke, 1984; Ancochea et al., 1994; Guillou et al., 1998; Carracedo et al., 1999; Camacho et al., 2009)

La Palma is currently in the growing shield-stage of volcanic oceanic islands (Carracedo, 1999). While the seamount below La Palma is up to ~4 Ma old (Staudigel & Schmincke, 1986), the island itself is between 1.7 and 2 Ma in age (e.g. Ancochea et al., 1994; Carracedo et al., 2001; Guillou, 2001; van den Bogaard, 2017). Volcanic activity has therefore been present during the whole duration of the existence of La Palma. In the last 500 years alone, seven eruptions have been recorded in Carracedo et al., (2001) and Longpré & Felpeto (2021), which both gather and review studies, maps and eyewitness accounts of the historic eruptions. The last eruption happened very recently at the end of 2021 (Longpré, 2021), which has been a typical Strombolian-type eruption (Carracedo et al., 2022) and the resulting volcano has been named “Tajogaite”.

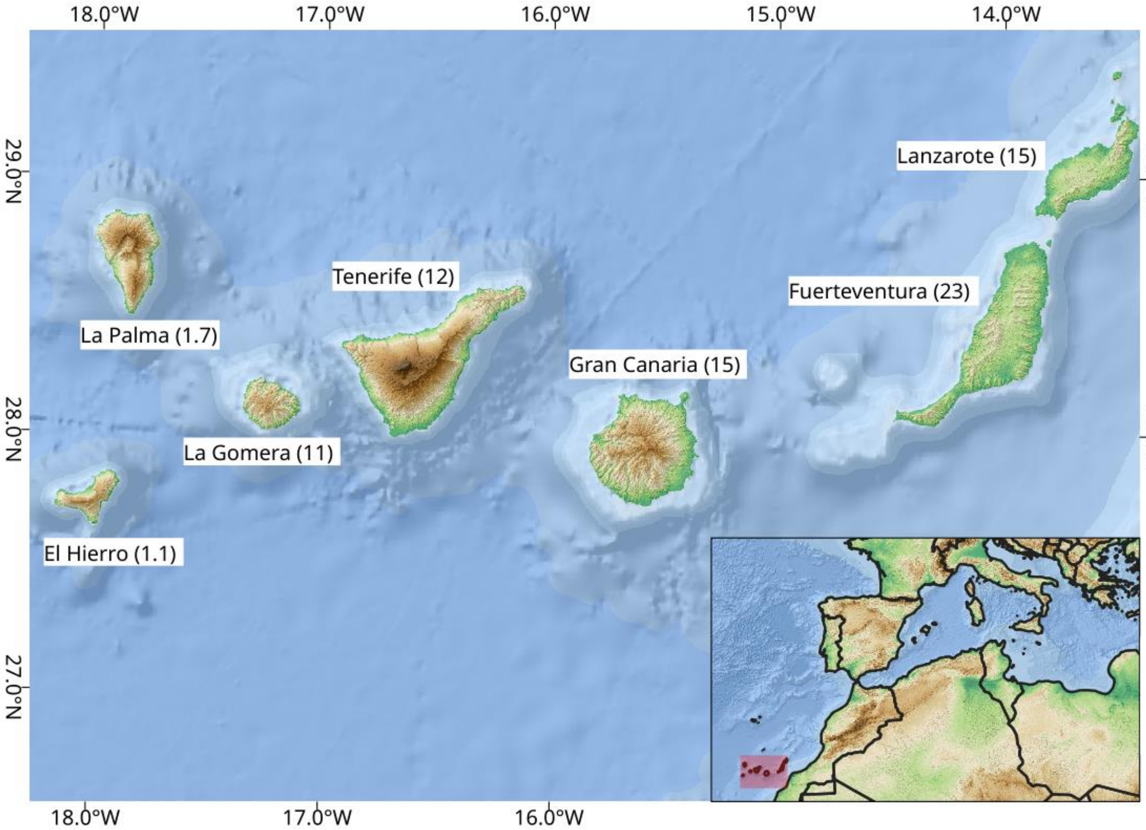

Figure 3. Overview over the seven main islands of the Canarian Archipelago with their age in million years in brackets. Island ages are according to van den Boogard, 2013. Source for topographic map: "SRTM30 colored" by terrestris.de and NASA EOSDIS Land Processes Distributed Active Archive Center (terrestris, 2023). Source for ocean basemap: "World Ocean Base" by Esri, Garmin, GEBCO, NOAA NGDC, and other contributors (Esri, 2023)

While geologic aspects of these volcanic eruptions are well investigated, only few studies exist on the major effect of these events on the vegetation (Dale et al., 2005), much less so specifically for islands. Genetic analysis have shown that colonizing species in situ evolved towards the currently endemic species (Juan et al., 2000), which means that endemic species evolved under the influence of volcanism. On the Canary Islands, volcanic activities have led to a diverse mosaic of different ages and structures (Figure 3). Different aspects of volcanism significantly contribute to the disturbance regime of La Palma on different temporal and spatial scales and can reach intensities, where all species on islands can go de facto extinct. Evidence suggests that this has happened on the neighbouring island of Gran Canaria during a period of violent volcanic activity called Roque Nueblo 5.6 - 3 Ma ago (Perez-Torrado et al., 1995; Emerson, 2003; Navascues et al., 2006), but this has been doubted as well (Anderson et al., 2009) and has been tested in Steinbauer et al., (2012) with models being significant both at an age of 14.4 and 3.5 Ma in age. On La Palma, there is evidence for large-scale landslides and debris avalanches, which can be initiated by volcanism (Siebert, 1984; Ancochea et al., 1994; Carracedo, 1999). Rockfalls are common, especially in the Caldera de la Taburiente (Carracedo, 1999). Evidence points at increasing instability of the western flank of Cumbre Vieja (Day et al., 1999) which - seen as an exaggeration by some authors (e.g. Carracedo, 2014) - could cause a large scale collapse of the western flank of La Palma (Ward & Day, 2001). Lava flows from past eruptions are now sites of succession (Irl et al., 2019) and old tephra layers are visible in many parts within and without of the Caldera. Volcanic activity therefore is an omnipresent part of the disturbance regime and influenced species diversity on several levels by significantly altering habitats. One example is the endemic *Pinus canariensis*, which has been shown to benefit from volcanic activity due to its resilience and ability to survive on arid volcanic soils (López de Heredia et al., 2014)

1.4.2.2 *Forest wildfires*

La Palma is among the few islands exhibiting a natural fire regime (Climent et al., 2004). Low amounts of charcoal present in sediment profiles show that fire frequency on the Canary Islands was low until the arrival of humans approximately 2400 - 2000 years ago (de Nasciemento et al., 2009, 2020). Before human arrival, fires were started by volcanic activity or lightning (Höllermann, 2000). Due to infrequent thunderstorms on La Palma, fires started by lightning strike only account for 0.4 - 0.5% of known fires (Höllermann, 2000; Climent et al., 2004). Another reason for the low fire frequency before human arrival is, that volcanic eruptions don't always cause fire. For example, the recent Tajogaite eruption has not caused any forest fires which is attributed by local scientists to a lack of oxygen during the eruption. While fires where rare in the past, they often covered large areas. After human arrival, the fire frequency increased dramatically (Nogué et al., 2013), leading to more but smaller fires (Molina-Terrén et al., 2016). In the 1960s, the fire regime changed again. Fire suppression and therefore fuel accumulation led to rare but large-scale fires, now linked to dry periods (Molina-Terrén et al., 2016).

Fire strongly affects the mineral contents of burned soils. After a short peak in nitrogen (N) (Durán et al., 2008), N levels decrease for more than 17 years (Durán et al., 2009; Durán et al., 2010), Phosphorous levels decrease first, but recover over time (Durán et al., 2008)

How well ecosystems on La Palma cope with fire varies considerably. The Canary Pine forests with *P. canariensis* as the most prominent species are well adapted to fire which will be discussed in more detail later. Evidence suggests that the increased fire frequency after human arrival contributed significantly to changes in the tree species composition of the islands (Galván, 1993; de Nasciemento et al., 2009), allowing *P. canariensis* to become dominant in many areas due to its developed adaptations to volcanism and fire. Fires often also spread into the alpine zone (Irl et al., 2012), where the summit scrub harbours a high number of endemic species (Irl & Beierkuhnlein, 2011). While endemic species on the Canary Islands are often poorly adapted to fire (Garzón-Machado et al., 2012), fire in the summit region nonetheless increases species richness (Irl et al., 2014).

Generally, while the Canary Pine forests on La Palma are close to their potential distribution (Arévalo et al., 2011), they are far from "natural". Changing this is a current goal of restoration on the island. However, the vast differences in forest structure, *P. canariensis* traits, soil properties and climatic properties make it a challenge to define a "natural" *P. canariensis* forest. Additionally, the recovery and understory structure of *P. canariensis* strongly changes with location and is not yet well understood. With climate change, an increase in the frequency of droughts is expected for the Canary Islands, which will lead to an increase in the fire frequency and negatively influence the recovery of *P. canariensis* due to drought stress (Figure 4).

Figure 4. Canary Pine stands between Volcán Martín and the town of Los Canarios showing discoloration due to drought stress (Photograph: Frank Weiser).

1.4.2.3 Invasive species and herbivory

Islands are exceptionally threatened by biological invasion, with the introduction of novel species identified as a major driver of biodiversity loss (Leclerc et al., 2018). The Canary Islands are more resistant to this than other archipelagos (Fernández-Palacios et al., 2023). Nonetheless, 682 of the 1161 plant species on La Palma are considered native, 479 non-native out of which 75 are invasive (Beierkuhnlein et al., 2021), with most invasive species originating from the Neotropics (Morente-López et al., 2023). Invasion has been aided by humans, which have been present on the islands of the archipelago since 2400 to 2000 years before present (de Nasciemento et al., 2020). In addition to invasive plants, introduced herbivores pose a threat to the local flora and fauna. Endemic species are often more heavily browsed than non-endemics (Cubas et al., 2019) and lack defence mechanisms due to an absence of herbivores in their evolution (Courchamp et al., 2003).

The introduced herbivores in turn profit from a lack of predators (Shea & Chesson, 2002). European rabbits (*Oryctolagus cuniculus*) pose an especially significant problem, have been introduced to more than 800 islands (Flux & Fullagar, 1992) and were listed among the 100 worst invaders (Lowe et al., 2000). On La Palma, rabbits influence the composition of the summit scrub by reducing seedling recruitment for endemic species except *Adenocarpus viscosus* ssp. *spartioides* (Webb & Berthel.) Rivas Mart. & Belmonte (Irl et al., 2012). In the pine forest, rabbits, barbary sheep (*Ammotragus lervia*) and goats (*Capra hircus*) negatively affect native endemic legumes in the species-poor understory communities (Garzón-Machado et al., 2010). Two endemic *Lotus* species, *Lotus pyranthus* P. Perez in the pine forest and *Lotus eremiticus* A. Santos on isolated rocks at the northern coast, have nearly been pushed to extinction by introduced herbivores. Both now show very little genetic variation in their remnant population (Pérez-Vargas et al., 2020). Considerable effort is invested into the protection of the species (Medina, 2021). Introduced rodents and other mammals prey on endemic birds in the laurel forest, disrupting seed-dispersal, and hunt endemic lizard species (Nogales et al., 2006; Traveset et al., 2009).

Invasive plants on the Canary Islands are confined to lower elevations below 1200 m a.s.l., peaking at around 500 m a.s.l. (Steinbauer et al., 2016). A prime example for plant invasion facilitated by human drivers is the grass *Cenchrus setaceus* (Forssk.), which is also known as *Pennisetum setaceum* (Forssk.) Chiov. which spreads mainly along roads. Theoretically, ~35% of the island all along the coasts and lower elevations are suitable for the species (Walentowitz et al., 2019). Another prominent example is the chestnut, *C. sativa*, has been introduced for agricultural purposes (Hernández-González et al., 2011) and is invading the laurel forest, as shown in **Manuscript 4,** even spreading into the Canary Pine forest, although frequent forest fires there make long term establishment unlikely. The spread into the laurel forest is especially problematic, as it poses a threat to a relic ecosystem which has survived since the tertiary period.

1.4.3 The Canary Pine forest – shaped by the disturbance regime

1.4.3.1 Past and current distribution of Pinus canariensis

The Canary Pine forest, the subject of most manuscripts in this thesis, is especially shaped by the disturbance regime. It covers 250 km² of the 708 km² of the island (35%, Figure 5), 208 km² of which are within a protected area. The tree layer is almost exclusively made up by *Pinus canariensis*, a species endemic to the Canary Islands, occurring on all islands apart from Fuerteventura and Lanzarote (Ceballos & Ortuño, 1951). Closely related taxa were common all over the Mediterranean basin and surroundings and have been found in fossils from Anatolia (Kasalpligil, 1977), Austrian fossils from the upper Miocene (Klaus, 1982; Klaus, 1984) and Alicante, Spain (Morla et al., 2002 as cited by Miranda, 2017). Its closest current relative in the genus *Pinus* is *Pinus roxburghii* Sarg. from the Himalaya (Critchfield & Little, 1966; Klaus & Ehrendorfer, 1989). It has been suggested, that the ancestor species of *P. canariensis* and *P. roxburghii* formed a belt along the Parathetys coast from present day Spain to Himalaya (Klaus, 1982), explaining the nowadays disjunct areal of the two closely related species after climatic changes and formation of the alps (de Navascués Melero, 2005). *P. canariensis* represents the transition towards more "modern" pine species compared to *P. roxburghii* (Gernandt et al., 2005) and shows strong variation in many morphological traits, especially cones (Gil et al., 2002; Tapias et al., 2004). On the Canary Islands, the first fossils from Gran Canaria dating the occurrence of the species or its predecessors are 13 Ma old (García-Talavera et al., 1995).

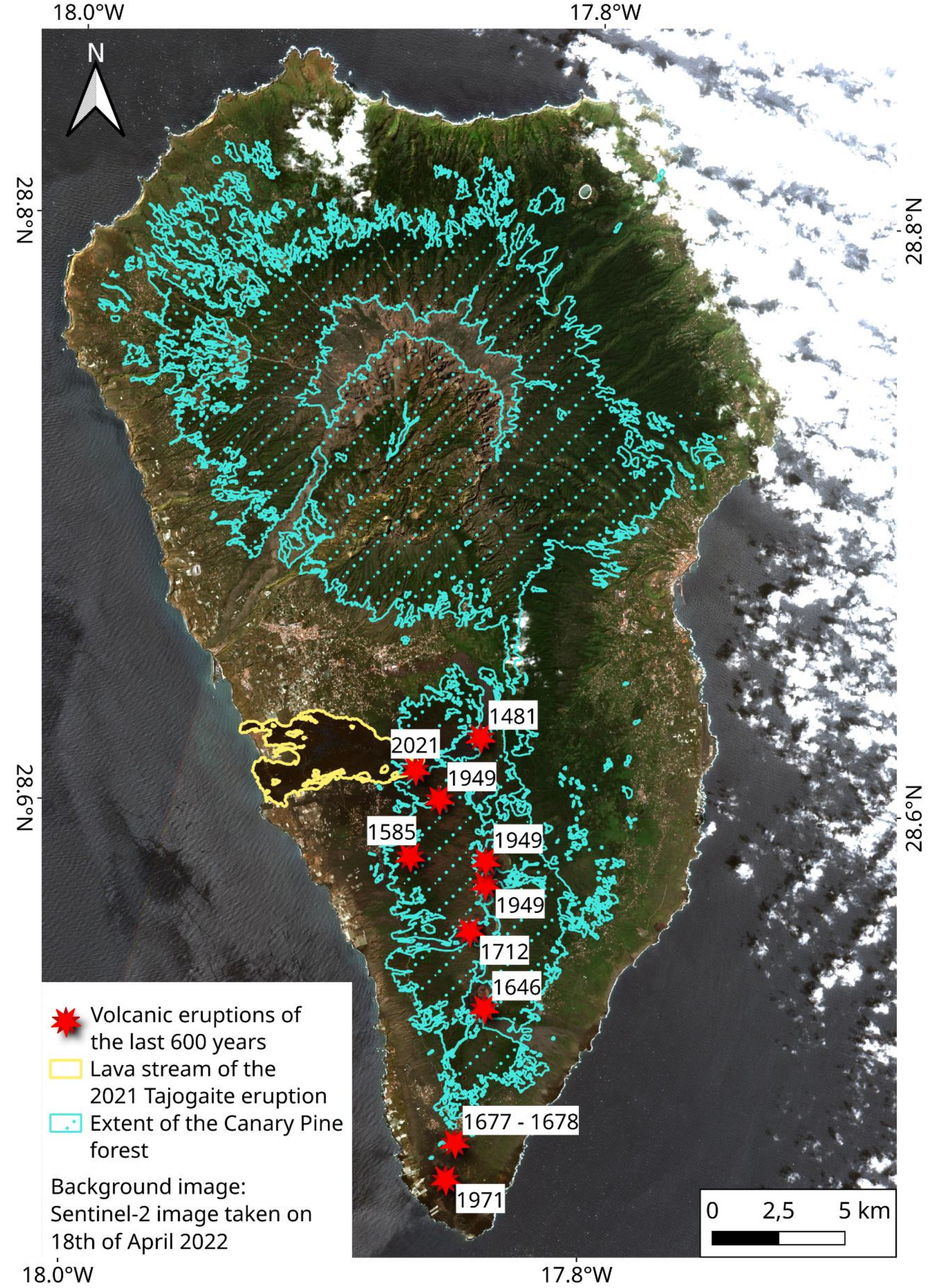

Figure 5: Current extent of the Canary Pine forest (turquoise) based on the classification by del Arco Aguilar et al. (2010), location of volcanic eruptions in the last 600 years (red stars) and the lava stream of the recent 2021 Tajogaite eruption (yellow) (Copernicus Emergency Management System, 2021). The background image is a Sentinel-2 image from 18th of April 2022.

While conditions on the Canary Islands were more humid in the past, even in the late Holocene (de Nasciemento, 2009), *P. canariensis* is able to grow in both dry and wet conditions covering a broad climatic envelope ranging from 300-1500 mm of annual precipitation (Blanco Andray et al., 1989; Brito et al., 2014). The species occurs from close to sea level up to the treeline at approximately 2300 m elevation (Miranda et al., 2021). Seasonal growth interruptions are common both at the upper and lower treeline, with most stable growth conditions in the cloud forest (Weigel et al., 2018). *P. canariensis* is very well adapted to dry conditions and periods of drought (Luis et al., 2005). Phenotypic plasticity has allowed provenances of the species from the leeward slopes of the island to adapt to dry conditions and droughts (López et al., 2013). Examples would be the strong resistance to cavitation developed on the leeward slopes of the islands (López et al., 2016), tap roots reaching up to 15m (Climent et al., 2007) and xeromorphic needles with different adaptions to dry conditions (Jiménez et al., 2000; Grill et al., 2004; Peters et al., 2008). On the eastern slopes, the trade winds drive clouds uphill, allowing fog to condense and precipitate on the long needles of *P. canariensis*, doubling the available water (Aboal et al., 2000). Even with all these adaptations, drought is the most limiting factor to tree growth (Jonsson et al., 2002; Wieser et al., 2016), with sensitivity changing between leeward and windward sides of the islands (Rozas et al., 2011).

P. canariensis forms the treeline on the Canary Islands. Many adaptations to dry environments (Stabentheiner et al., 2004) and frost (Luis et al., 2007) allow it to survive in the harsh conditions of the treeline ecotone. Nonetheless, the treeline is roughly 1000 m lower compared to the Atlas Mountains, the next continental mountain range. The reasons could be anthropogenic destruction of *Juniperus cedrus* Webb & Berthel dwarf forests by human use (Höllermann, 1978; Santos Guerra, 1983) or isolation itself causing the lack of a suitable high-altitude tree species ever reaching the island (Leuschner, 1996). Another theory is, that the treeline on the Canary Islands is possibly drought induced (Gieger & Leuschner, 2004), which is under debate (Rozas et al., 2013). Precipitation and therefore growth of the species are strongly linked to the North Atlantic Oscillation (NAO) (Rozas et al., 2013), which is expected to change in the coming decades (Hurrell & Deser, 2010). This change already leads to an increase in droughts in the Mediterranean (Hoerling et al., 2012) and will lead to more frequent and severe droughts in the future (López-Moreno et al., 2011; Tramblay et al., 2020; IPCC, 2023).

1.4.3.2 *Adaptations of* Pinus canariensis *to disturbances*

Pinus canariensis is well adapted to disturbances, such as fire. It is among the, if not the most resistant pine species globally (Fernandes et al., 2008). In line with other studies (de Ronde, 1982; Climent et al., 2004) one study reports a 100% survival rate one year after a fire even in high severity burn areas (Otto et al., 2010). The canopy of *P. canariensis* forests recovers quickly after fires, with only minor differences in canopy cover visible three and a half years after fire (Arévalo et al., 2001). Adaptions to fire include reserve carbohydrates in the sapwood parenchyma cells (Climent et al., 1998), thick bark, large, well-protected buds, the ability to resprout from all above-ground parts and serotinous cones (Climent et al., 2004). The species shows both traits helping fire survival (thick bark, resprouting) and recolonization (serotinous cones). Being able to resprout from epicormic buds in the stem is a rather uncommon adaption found in systems adapted to moderate to high fire intensities with a high frequency (Pausas & Keely, 2017).

P. canariensis is genetically highly variable. How developed traits related to fire (e.g. serotinous cones or bark thickness) are, is strong linked to the fire regime in the area. Climent et al. (2004) found thicker barks in areas with productive, dense forest stands and frequent high intensity fires. Thinner barks were found in sparser pine stands, where most fires are ground fires burning the litter layer. Those varying extents of fire adaptation are of interest to determine the extent of influence of fire regimes in plant evolution (Pausas & Schwilk, 2012).

Canary Pine forests of a certain age are almost single species stands in the canopy layer. The understory usually only harbours a comparatively small number of species (only approximately 19% of species are present, but the pine forest covers 35% of the area), but with a high degree of endemism (see Table 2 based on Beierkuhnlein et al., 2021). Additionally, nearly three quarters of endemic species in the pine forest exhibit woodiness, which is a trait very common on islands with the reason under discussion (Nürk et al., 2019; Hooft van Huysduynen et al., 2021; Zizka et al., 2022).

Table 2: Number of species on La Palma and in the Canary Pine forest as well as the percentage of endemic species. Endemic species are split into single island endemics (SIE) only occurring on La Palma and multi-island endemics (MIE) also existing on other islands of the archipelago. The percentage values given in the last two rows are not the percentage of total species but the percentage of endemic species that are woody or nitrogen fixers. Species categorization is based on Beierkuhnlein et al., 2021.

	La Palma (total)		**Canary Pine Forest**	
Plant species	1161		223	19.21% (of total)
Endemic species	208	17.92%	118	52.91%
MIE	161	13.87%	83	37.22%
SIE	47	4.05%	35	15.7%
Woody species	332	28.6%	113	50.67%
Nitrogen fixer	104	8.96%	19	8.52%
Endemic woody species	136	65.38% (of endemics)	85	72.03% (of endemics)
Endemic nitrogen fixers	18	8.66% (of endemics)	12	5.38% (of endemics)

2 Remote sensing as an emerging approach in island biogeography

2.1 Remote sensing in biodiversity monitoring

Understanding biodiversity patterns and their environmental drivers has been the focus of biogeography for centuries. Investigating these patterns is becoming more urgent with the challenges of the ongoing global changes. Gathering representative datasets to understand global trends is prohibitively expensive or time consuming. These issues have been alleviated in recent decades by the rise of remote sensing. Advancements in spectral, spatial and temporal resolution have steeply increased the usefulness of remote sensing for ecologists (Turner et al., 2003; Wang & Gamon, 2019; Cavender-Bares et al., 2022). Remotely sensed data can be used for different purposes. For example, remote sensing can provide auxiliary data for studies analysing field data, such as digital elevation models (e.g. SRTM (Rodriguez et al., 2006; van Zyl, 2001) or ASTER (Tachikawa et al., 2011)), land cover information or change detection (Kerr & Ostrovsky, 2003). Hundreds of spectral indices, which are calculated from different spectral bands of optical satellites, exist for hundreds of different ecological applications. One relatively simple index is the Normalized Difference Vegetation Index (NDVI), which is calculated from the ratio of the reflectance of red wavelengths (RED) and the near infrared (NIR).

$$NDVI = \frac{NIR - RED}{NIR + RED}$$

Despite its many disadvantages and simplicity, it can be and is successfully used for a multitude of purposes (Pettorelli, 2013; Zeng et al., 2022). As it is a proxy for photosynthetic activity, it is used to monitor productivity, phenological parameters (Pettorelli et al., 2005; Cleland et al., 2007), as a predictor variable for animal population models (Pettorelli et al., 2011) and in disturbance monitoring, e.g. for volcanic eruptions (e.g. Houlié et al., 2006; Raynolds et al., 2015; Easdale et al., 2018; Corradino et al., 2022).

In recent years, remote sensing has also been employed to directly monitor biodiversity based on differences in spectral patterns. Assessing species richness with ground surveys is time and labour intensive, always biased and influenced by different choices, such as sampling design, study area and definitions (Chiarucci, 2007; Chiarucci et al., 2011). Remote sensing offers a way to efficiently and frequently monitor biodiversity while reducing many of these biases (Gillespie et al., 2008; Wang & Gamon, 2019). Remote sensing data can serve as a data basis for species distribution models (He et al., 2015), improve them by including a temporal, process oriented component (Randin et al., 2020), be used to monitor essential biodiversity variables (EBVs) (Skidmore et al., 2015; Jetz et al., 2019; Skidmore et al., 2021), contribute to the targets set by the Convention on Biological Diversity (CBD) (Cavender-Bares et al., 2022) and can often be directly connected to species diversity on the ground (e.g. Féret & Asner, 2014). α and β-diversity are linked to the concept of "spectral species", where species exhibit a distinct spectral reflectance signature.

Species can be distinguished by investigating the spectral reflectance patterns of the pixels of a remotely sensed image and can be used as a proxy for α-diversity and then also to calculate β-diversity metrics (Rocchini et al., 2022a, 2022b). This approach can be supported by other dataset types, such as radar or LiDAR improving accuracy by providing structural parameters (e.g. Simonson et al., 2012; Torresani et al., 2020). However, the concept of spectral species is strongly dependent on spatial scale, as depending on species size and image resolution, pixels often contain a mix of species and therefore not necessarily represent single species but often species assemblages (Rocchini et al., 2021). It is also linked to the concepts of the "Spectral Variation Hypothesis" (Palmer et al., 1999, 2002) where higher spectral heterogeneity represents higher niche heterogeneity and can therefore – depending on scale (Rocchini et al., 2018)- be used as a proxy for species diversity (Rocchini et al., 2010).

Remote sensing is well suited to investigate both species richness and habitat heterogeneity (Warren et al., 2014; Peng et al., 2018) and is generally an important tool for ecologists to efficiently monitor global biodiversity and its loss (Pettorelli et al., 2014). Overall, remote sensing as a method to monitor and assess biodiversity is well established and used with great success. Especially in combination with field survey data it poses an important tool for ecologists to efficiently monitor global biodiversity and its loss (Pettorelli et al., 2014).

2.2 Remote sensing on the rise

While remote sensing data and methods have been in use for decades and the necessity of remote sensing in biodiversity monitoring is becoming more apparent, the biggest catalyst for the rise in usage is the growing amount of openly available data. The number of satellite constellations has steadily increased since the 1970s and is still increasing. The European Union adds to this wealth of data with the Copernicus programme (Jutz & Milagro-Pérez, 2020). Its components cover a wide range of applications and satellite types and aims at being "the most comprehensive Earth observation system worldwide" (Showstack, 2014). The included Sentinel satellite constellations provide data for Earth system models (Berger et al., 2012). This includes broad applications, such as the radar mission Sentinel-1 (Torres et al., 2012), the optical high-resolution Sentinel-2 satellites (Drusch et al., 2012), and the medium-resolution optical Sentinel-3 constellation (Donlon et al., 2012). These are complimented by satellites with a more specific application, such as Sentinel-5P for air quality monitoring (Veefkind et al., 2012).

Another important optical dataset is the Landsat-constellation, which offers data with a time series since 1972 and is cost-free since 2008. The mission has recently been continued by Landsat 8 and 9 (Roy et al., 2014; Masek et al., 2020). As the longest running optical satellite mission it offers the unique opportunity to monitor long-term change with a high spatial and temporal resolution. The Moderate Resolution Imaging Spectroradiometer (MODIS) on the satellites Terra and Aqua offers medium resolution images with a very high temporal resolution (Justice et al., 2002a) and many pre-processed products, such as fire products (Justice et al., 2002b), vegetation indices (Huete et al., 1999) or snow products (Hall et al., 2002).

This wealth of openly available data is complemented by an increasing number of commercial providers. While many commercial datasets are not available for free usage which hinders scientific progress (Turner, 2013), more and more providers offer free data quotas for scientific purposes, e.g. PlanetScope data (Planet, 2019; Frazier & Hemingway, 2021). PlanetScope is also an example for another strategy in Earth observation: Instead of few, expensive satellites with a high risk of failure (like the failed launch of Landsat 6 or the mechanical failure of Landsat 7, which significantly reduced data quality after 2003), small satellites like CubeSats (Poghosyan & Golkar, 2017; Crusan et al., 2019; Villela et al., 2019) offer advantages, such as cheap production cost, high revisit times and lower susceptibility to data gaps if parts of the constellation fail.

Technological developments further increase the availability of data. Increasing capabilities hand in hand with falling prices have led to a rapid increase in the use of Unmanned Aerial Vehicles (UAV) for remote sensing (Colomina & Molina, 2014). UAVs make very high-resolution remote sensing data from a multitude of different sensors much easier to gather than in the past. In addition, apart from sensors, UAVs can also carry other instruments able to measure relevant environmental parameters. In a novel approach, UAVs have recently been used to sample endangered plants from steep cliffs virtually impossible to access for humans (La Vigne et al., 2022).

Other advances include the EnMap mission, which provides hyperspectral data to the public (Guanter et al., 2015), for which in the past expensive overflights with airborne sensors on planes were typically necessary. This advance is especially important for biodiversity research as hyperspectral data is well suited to detect plant species richness (Lucas & Carter, 2008).

This broad range of datasets is also a necessity, as all remote sensing products are always a trade-off between spatial, spectral and temporal resolution. Images of very high spatial resolution often only cover a small area and have lower revisit times and vice versa. Table 3 illustrates the trade-off for three common optical satellite constellations/sensors, Landsat, which offers the longest time series, MODIS, which offers the highest temporal resolution and Sentinel-2, which offers the highest spatial resolution of the three and a high temporal resolution but currently only a short time series. While this makes special consideration necessary when designing a study, it also allows researchers to investigate biodiversity on many different scales. Additionally, the combination of different datasets offers the possibility to investigate research questions from different angles.

Table 3: Properties of three prominent satellite constellations. Values stated for Landsat are for the currently active satellites, Landsat 8 and 9 with Operational Land Imager (OLI) sensor. Past satellites had lower revisit times, data gaps and different sensors with different spatial and spectral resolution.

Constellation/Sensor	**Landsat**	**MODIS**	**Sentinel-2**
Spatial resolution	30 m	250/500/1000 m	10/20/60 m
Temporal resolution	8 days	Daily/8 days/16 days	5 days
Time series	Since 1972	Since 1999	Since 2015

2.3 Usage in island biogeography

One defining trait of islands is their isolation, which is included in many of the aforementioned models and theories of island biogeography. Many oceanic islands are therefore hard to reach, especially when not developed for tourism. Additionally, due to the volcanic origin of many oceanic islands, they are often characterized by complex topography. Mouillot et al., (2020) also calculated, that 22% of island area is under protection status, with 14.4% of investigated islands having >90% of their area protected. Field surveys in protected areas are often - depending on protection level - further complicated by permit procedures. Both isolation and logistical difficulties hold especially true for biodiversity hotspots, e.g. the Galapagos Islands. Additionally, some habitats for endemic species are sensitive to disturbances and even the most careful on-site sampling could drastically damage and alter the sampled habitat. Another important circumstance is that habitats for endemic species can be spatially restricted, where the direct interaction with the habitat should be kept to a minimum to not risk driving the endemic target species to extinction.

Combined, remoteness and topography make field surveys on islands more time, labour and cost intensive compared to studies on continents. Island biogeography can therefore profit exceptionally from the efficient, easy to repeat monitoring possibilities remote sensing offers.

Unfortunately, some disadvantages of remote sensing are amplified by island characteristics. Complex topographies with steep slopes often require special attention during pre-processing (Riaño et al., 2003; Weiss & Walsh, 2009) and areas close to vertical cliffs and valley walls are not visible depending on the look angle of the used satellite dataset. Shadows often make illumination correction necessary (Meyer et al., 1993) and images must be corrected for sloped geometries (Itten & Meyer, 1993). In general, remote sensing on high elevation islands requires the same pre-processing procedures as continental mountain environments and still suffers from a high rate of image artifacts. Radar images encounter problems in steep valleys with radar layovers and shadows (Eineder & Holzner, 2000; Ludwig & Schneider, 2006; Kolecka & Kozak, 2014).

Another issue with optical remote sensing on islands is the high frequency of cloud cover on some islands. The Canary Islands are situated in the north-east trade winds (Fernandopullé, 1976). On La Palma, this leads to frequent cloud cover on the north-eastern and eastern slopes of the islands (Garzón-Machado et al., 2014). The clouds do not reach the high elevation zone of the island due to the trade wind inversion and the ridge of Cumbre Nueva keeps clouds from reaching the islands western part. This leads to a complex mosaic of cloud cover with vastly different rates of image availability also depending on elevation. Similar challenges are known from other Archipelagos, e.g. Hawaii (Cao et al., 2007). The increasing number of satellites alleviates this problem by higher revisit frequencies.

Nonetheless, the advantages of remote sensing for island biogeography vastly outweigh the restrictions and difficulties to overcome. An increasing number of studies make use of remote sensing to successfully investigate different aspects of island biogeography, such as β-diversity patterns (e.g. Rocchini et al., 2018; Hoffmann et al., 2019; Feret & De Boissieu, 2020).

3 Outlook

3.1 Emerging questions related to disturbances and their effects

1. The 2021 eruption of Tajogaite caused severe damage to the Canary Pine forest. While all affected individuals of *Pinus canariensis* were resprouting during the fieldwork for **Manuscript 2** and **3**, many severely affected trees had already resprouted for the third time in April 2022, five months after the end of the eruption. While *P. canariensis* is typically very resilient, resprouting this often is a significant investment of resources. It therefore remains to be seen if the affected trees can profit from their extraordinary resilience to fire, which allows it to fully recover within a few years and recover from chlorotic damage equally well, or if the current resprouting is a last attempt at survival.
2. Sulphur gasses affecting island ecosystems after volcanic eruptions are so far little studied. While some studies exist in the context of anthropogenic sulphur sources and terrestrial eruptions, such as Mount St. Helens, the large amounts of sulphur emitted during the Tajogaite eruption affected all surrounding ecosystems. Additionally, the tephra layer will leach sulphur for many months. It remains to be seen how existing communities adjust to this.
3. Large amounts of tephra were deposited during the last eruption and covered many different species. First observations in the field showed high survival rates of woody, endemic species while herbaceous vegetation disappeared. Monitoring long term survival of both endemic and non-endemic species and patterns of recovery of the vegetation will allow insights into the development of the still debated creation of insular woodiness, which has recently been attributed to be influenced by tephra cover (Beierkuhnlein et al., 2023).
4. Similar to overlapping environmental gradients shaping diversity patterns, disturbances rarely are a singular event. To properly understand diversity patterns, the disturbance

history and especially different disturbances affecting the same community need to be considered. In the case of the recent Tajogaite eruption, sulphur gases and ash deposits have affected communities that were recently exposed to drought and six years before that wildfire.

5. While *Pinus canariensis* is well adapted to drought, an increase in their occurrence with climate change is expected and has already been observed in recent years. It is unclear, how this change will influence the distribution of pine forests, especially in the harsh treeline ecotone.

3.2 Emerging questions related to combining remote sensing and in-situ data

6. The "Spectral Variation Hypothesis" links variation in spectral reflectance patterns of satellite images to biodiversity on the ground. It has been successfully employed to assess β-diversity patterns for some plant communities on the north-western coast of La Palma (Hoffmann et al., 2019). Extending this approach to the whole island would yield important insights into the opportunities and limits of remote sensing in biodiversity research.
7. UAVs offer many new opportunities. Along the northern coast of La Palma, steep barrancos host endemic species (Cutts et al., 2019) and are even a refugium for nearly extinct endemics such as *Lotus eremiticus*. Many of the steep slopes are not accessible for humans and too steep to investigate by satellite images. UAVs offer opportunities for in depth analysis of the diversity of these barrancos and can even be used to take individual species samples with recent developments, paving the way for new insights in these unique habitats.
8. The recently launched EnMAP satellite mission provides free hyperspectral data to the scientific community. The high spectral resolution of EnMAP compared to common multispectral sensors such as Sentinel-2 or Landsat 8 and 9 will allow many new opportunities, such as improved β-diversity mapping or more sensitive detection of plant stress, which will need to be tested and fully explored.

4 Synopsis

4.1 Synthesis of the manuscripts

As discussed before, the role of disturbances in island biogeography is not paid due attention (Whittaker & Fernández-Palacios, 2007). La Palma offers many opportunities to research how past disturbances shape current patterns of biodiversity as well as direct impacts of current disturbances. One ecosystem especially shaped by disturbances is the Canary Pine forest. While comparatively species poor in the understory vegetation, the degree of endemism is very high (Beierkuhnlein et al., 2021). Fire is a common occurrence in these forests, especially since human arrival and land use increased the frequency of the fire regime (Molina-Terrén et al., 2016). Fires also offer understory species a brief opportunity to thrive by removing the dense litter needle litter layer and setting resources free. The goal of the first manuscript was therefore to assess patterns of α- and β-diversity using data sampled after a fire:

Manuscript 1 investigates how fire intensity during the 2016 wildfire, which occurred mostly on the western slopes of Cumbre Vieja, influenced understory α- and β-diversity. The Canary Pine forests, in which the tree layer is almost exclusively formed by *Pinus canariensis*, is typically rather species poor. Understory vegetation is limited by the dense, thick little layer formed by long needles shed by *P. canariensis* as well as a lack of light and nutrients. *P. canariensis* is well adapted to fire and able to survive and resprout even after the most severe burns. Nonetheless, in the years between a fire and the full recovery of *Pinus*, higher resource availability offers a window for increased species richness. We investigated how fire intensity (derived from Sentinel-2 remote sensing images) impacts species richness and β-diversity. Given the rapid recovery and fire adaption of *P. canariensis*, it is very hard to assess fire intensity and severity of fire effects in the field. Therefore, remote sensing offered a more objective way to quantify fire intensity, which only had a minor influence on species composition. Elevation, most likely as a proxy for changing precipitation patterns, was more important for the composition of understory vegetation 1.5 years after the fire. Additionally, the endemic species *Lotus campylocladus* ssp. *hillebrandii* (Christ) Sandral & D. D. Sokoloff forms thick patches strongly influenced understory composition, leading to significantly lower species numbers in plots where it was present. Overall, we were able to show the importance of elevation (as a proxy for e.g. the precipitation regime) and *Lotus campylocladus* ssp. *hillebrandii* for understory species richness after the 2016 fire, which were more important than fire intensity.

The 2021 Tajogaite eruption offered the unique opportunity to directly investigate effects of a volcanic eruption on these forests. Given the good experiences made with Sentinel-2 NDVI products in **Manuscript 1**, which offered a reliable way to assess suffered canopy damage with high spatial resolution, I used a similar approach to analyse patterns of chlorotic damage in the forests affected by the volcanic eruption as soon as images not affected by the volcanic plume were available after the end of the eruption:

Manuscript 2 uses Sentinel-2 images to investigate chlorotic damage suffered by *P. canariensis* during the 2021 eruption of the volcano Tajogaite on La Palma. During the eruption, which lasted from 19th of September to 13th of December 2021, more than 1 million tonnes of SO_2 were emitted (Rodríguez et al., 2023). The increased levels of sulphur poisoned Canary Pine forests around the craters, leading to severe chlorotic damage. Our results show that a circular area with approximately 7 km radius was affected by chlorosis, representing 10% of the Canary pine forests of La Palma. Intensity of damage was assessed using the Normalized Difference Vegetation Index (NDVI) as a proxy, which is a good indicator for plant health. The most important predictor for suffered chlorotic damage was the distance to the eruption site. The spatial pattern of damage was weakly directional because of weak wind speeds throughout the duration of the eruption.

After the end of the volcanic eruption, rapid resprouting was visible in most Canary Pine trees. Even severely damaged trees were resprouting and showed signs of recovery. It is unclear, if the resprouting is the first signs of long-term recovery or if a large proportion of affected trees will not survive the following years. The affected trees need vast amounts of resources for their extensive resprouting, and this depletion of vital resources could be cause of elevated tree mortality. However, *P. canariensis* is a commonly found colonizer on recent volcanic soils and is often resource limited (e.g. by nitrogen availability) in its growth (Durán et al., 2010a, 2010b; López de Heredia et al., 2014), making a full recovery of most trees likely. We sampled needles five months after the eruption for their nitrogen, carbon and sulphur levels to assess the nutrient status of the affected trees. These field measurements were also combined with an extension of the data processed for **Manuscript 2** to detect links between remotely sensed canopy status and needle properties:

In **Manuscript 3** we investigated the levels of sulphur (S), nitrogen (N) and carbon (C) in 100 needle samples after the 2021 eruption. 80 of those samples were situated within 7 km of the eruption, the other 20 further away. We used generalized additive models (GAMs) to disentangle the effects of several drivers (e.g. topography, tephra depth, distance to the eruption) on needle composition. We found significantly increased S levels in the sampled needles due to emissions of volcanic gasses throughout the eruption, leading to lowered C levels, which is translocated as a "building block" during recovery and resprouting of affected trees. N levels were linked to S content of needles but exhibited a much less clear pattern. A group of trees which were unburnt during the 2016 fire but close to the volcano strongly affected the model with their high S and N levels. Topography had little to no effect on the S, N, C composition in the sampled needles. We also modelled the tephra layer over the whole island from a combination of field measurements and an existing digital surface model. The effects of tephra, which also leaches deposited volcanic particles and changes water availability, was heavily linked to distance and had less explanatory power. Therefore, distance to the crater rather than the thickness of the tephra layer was used in our models. Overall, S, N and C levels were affected by a complex mixture of lasting wildfire effects from 2016, topographic exposure, tree health before the eruption and other factors hard to disentangle. We also investigated the link between the Sentinel-2 Normalized Difference Vegetation Index (NDVI), a proxy for vegetation health, at different times after the eruption and the measured needle elemental content. We did not find a significant correlation. While both damage and recovery are clearly visible in the processed satellite images, the missing link to S, N and C in needles can be explained by plant physiological processes too nuanced to be visible in remote sensing imagery, such as translocation of C and N during resprouting. The lack of correlation between our in-situ data and the remote sensing analysis shows the mutual benefit of combining both approaches, with remote sensing allowing efficient monitoring of overall damage patterns and field data relating to local processes on an individual level.

The final manuscript of this thesis stands in contrast with **Manuscript 1-3** as it investigates the laurel forest instead of the Canary Pine forest and invasion instead of disturbances. The manuscript is included in this thesis for the second goal of the thesis, to show how a combination of remote sensing and field data can be successfully used for many aspects important for island biogeography. And while **Manuscript 1-3** focused directly on disturbances, invasive species often profit from the higher susceptibility of endemic species to disturbance caused damage and mortality. **Manuscript 4** uses field data as ground truth for a remote sensing-based assessment of the current spread of an invasive species threatening to replace the relic laurel forest. The calculated current extent of the invasive species is then combined with species distribution models to map possible future habitats. **Manuscript 4** therefore shows how island biogeography can benefit from a combined approach of field work, remote sensing and modelling:

Manuscript 4 employs remote sensing and modelling to monitor a major threat to island biodiversity: invasion. We model the current and projected future extent of the invasive *Castanea* *sativa* on La Palma. Introduced for agricultural use, the species invades and threatens the laurel forest. In contrast to native tree species, *C. sativa* has not yet adapted to the lack of pronounced seasons on La Palma and is deciduous while the rest of the tree species on La Palma are evergreen. This leads to a very distinct spectral response pixels covered by the species when comparing images from summer and winter. This allows mapping the invasive tree with high accuracy, which was done here using a combination of Sentinel-2 and Landsat 8 images. The remote sensing derived current extent was then used to train species distribution models to obtain the theoretical environmental niche of *C. sativa*. Overall, it currently covers 1.2% of the area of La Palma, with 12-17% being theoretically suitable. Therefore, we were able to show and locate current hotspots of invasion on the island and able to identify vulnerable areas. These results could be directly translated towards meaningful conservation measures.

5 Declaration of my contributions to each manuscript

Manuscript 1

Title: Impacts of Forest Fire on Understory Species Diversity in Canary Pine Ecosystems on the Island of La Palma

Authors: Frank Weiser, Anna Sauer, Daria Gettueva, Richard Field, Severin D.H. Irl, Ole R. Veetas, Alessandro Chiarucci, Samuel Hoffmann, José Maria Fernández-Palacios, Rüdiger Otto, Anke Jentsch, Antonello Provenzale, Carl Beierkuhnlein

Journal: Forests 12(12), 1638; https://doi.org/10.3390/f12121638

Year: 2021

Personal contribution: Idea and concept: 60%, field work: 50%, data pre-processing: 100%, data analysis and figures: 100%, writing: 90%, corresponding author

Contributions of other authors: Conceptualization, C.B., R.F. and F.W.; methodology, C.B., A.S., D.G. and F.W.; validation, F.W., A.S., D.G.; formal analysis, F.W.; investigation, F.W., A.S., D.G., C.B.; resources, C.B. and A.J.; data curation, F.W.; writing—original draft preparation, F.W., A.S., D.G., S.H.; writing—review and editing, C.B., F.W., S.H., A.J., R.F., O.V., A.C., A.P., S.D.H.I., R.O., A.S., J.M.F.-P., R.O.; visualization, F.W.; supervision, C.B.; project administration, C.B.; funding acquisition, C.B., A.J.

Manuscript 2

Title: Impact of Volcanic Sulfur Emissions on the Pine Forest of La Palma, Spain

Authors: Frank Weiser, Esther Baumann, Anke Jentsch, Félix Manuel Medina, Meng Lu, Manuel Nogales, Carl Beierkuhnlein

Journal: Forests 13(2), 299; https://doi.org/10.3390/f13020299

Year: 2022

Personal contribution: Idea and concept: 80%, data pre-processing: 100%, data analysis and figures: 80%, writing: 70%, corresponding author

Contributions of other authors: Conceptualization, C.B. and F.W.; methodology, F.W., E.B. and C.B.; validation, F.W.; formal analysis, F.W.; investigation, F.W., E.B. and C.B.; resources, C.B. and A.J.; data curation, F.W.; writing—original draft preparation, C.B. and F.W.; writing—review and editing, C.B., F.W., E.B., F.M.M., M.N., A.J. and M.L.; visualization, F.W. and E.B.; supervision, C.B.; project administration, C.B.; funding acquisition, C.B.

Manuscript 3

Title: Combining in-situ monitoring and remote sensing to detect spatial patterns of volcanic sulphur impact on pine needles

Authors: Frank Weiser, Anna Walentowitz, Esther Baumann, Christopher Shatto, María Guerrero, Anke Jentsch, Manuel Nogales, Felix Medina, Ole R. Veetas, Carl Beierkuhnlein

Journal: Submitted to Forest Ecology and Management

Year: 2022**Personal contribution:** Idea and concept: 30%, field work: 30%, data preparation: 50%, data analysis and figures: 80%, writing: 70%, corresponding author

Contributions of other authors: Conceptualization: F.W., A.W. and C.B.; methodology: F.W., A.W. and C.B.; formal analysis: F.W., A.W. and C.S.; investigation: F.W., A.W., C.B. and A.J.; data curation: F.W., writing - original draft: F.W., A.W., E.B., C.S. and C.B., writing – review and editing: F.W., E.B., C.S., M.G.C., A.J., M.N., F.M.M., O.R.V. and C.B.; visualization: F.W. and A.W.; funding acquisition: F.W., A.W., A.J. and C.B.; project administration: C.B.

Manuscript 4

Title: Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island

Authors: Ram Sharan Devkota, Richard Field, Samuel Hoffmann, Anna Walentowitz, Félix Manuel Medina, Ole R. Veetas, Alessandro Chiarucci, Frank Weiser, Anke Jentsch, Carl Beierkuhnlein

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Year: 2020

Personal contribution: data acquisition 10%, data analysis 10%, visualization, 0%, writing 10%, idea and concept 20%

Contributions of other authors: Conceptualization, C.B. and A.J.; methodology, C.B., R.F., and R.S.D.; validation, R.S.D., A.W., S.H., and F.W.; data curation, R.S.D. and C.B.; writing R.S.D., C.B., R.F., S.H., and A.W.; review and editing, A.C., O.R.V., S.H., F.M.M., R.F., and A.J.; visualization, R.S.D. and A.W.; supervision, C.B.; project administration, C.B.; funding acquisition, C.B.

6 Manuscripts

6.1 Manuscript 1

Pinus canariensis stands six years after the 2016 fire

Impacts of Forest Fire on Understory Species Diversity in Canary Pine Ecosystems on the Island of La Palma

Published in: Forests, *12*, 1638 (2021)

Authors: Frank Weiser [1,*], Anna Sauer [2], Daria Gettueva [3], Richard Field [4], Severin D. H. Irl [5], Ole Vetaas [6], Alessandro Chiarucci [7], Samuel Hoffmann [1], José María Fernández-Palacios [8], Rüdiger Otto [8], Anke Jentsch [9], Antonello Provenzale [10] and Carl Beierkuhnlein [1,11,12]

Affiliations:

[1] Department of Biogeography, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany;

[2] Department of Agroecology, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany;

[3] Climate Policy, adelphi, Alt-Moabit 91, 10559 Berlin, Germany;

[4] School of Geography, University of Nottingham, Nottingham NG7 2RD, UK;

[5] Biogeography and Biodiversity Lab, Institute of Physical Geography, Goethe-University Frankfurt, Altenhöferallee 1, 60438 Frankfurt am Main, Germany;

[6] Department of Geography, University of Bergen, 5020 Bergen, Norway;

[7] BIOME Lab, Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum, University of Bologna, 40126 Bologna, Italy;

[8] Departamento de Botánica, Ecología y Fisiología Vegetal, Universidad de La Laguna, 38200 San Cristóbal de La Laguna, S/C de Tenerife, Spain;

[9] Disturbance Ecology, Universitätsstraße 30, 95447 Bayreuth, Germany;

[10] Institute of Geosciences and Earth Resources, National Research Council of Italy (CNR), Via G. Moruzzi 1, 56124 Pisa, Italy;

[11] Bayreuth Center of Ecology and Environmental Science BayCEER, Dr. Hans-Frisch-Straße 1-3, 95448 Bayreuth, Germany

[12] Geographical Institute Bayreuth GIB, Universitätsstraße 30, 95447 Bayreuth, Germany

*** Correspondence**: frank.weiser@uni-bayreuth.de

Abstract

Forest fires are drivers of spatial patterns and temporal dynamics of vegetation and biodiversity. On the Canary Islands, large areas of pine forest exist, dominated by the endemic Canary Island pine, *Pinus canariensis* C. Sm. These mostly natural forests experience wildfires frequently. *P. canariensis* is well-adapted to such impacts and has the ability to re-sprout from both stems and branches. In recent decades, however, anthropogenically caused fires have increased, and climate change further enhances the likelihood of large forest fires. Through its dense, long needles, *P. canariensis* promotes cloud precipitation, which is an important ecosystem service for the freshwater supply of islands such as La Palma. Thus, it is important to understand the regeneration and vegetation dynamics of these ecosystems after fire. Here, we investigated species diversity patterns in the understory vegetation of *P. canariensis* forests after the large 2016 fire on the southern slopes of La Palma. We analyzed the effect of fire intensity, derived from Sentinel-2 NDVI differences, and of environmental variables, on species richness (alpha diversity) and compositional dissimilarity (beta diversity). We used redundancy analysis (dbRDA), Bray–Curtis dissimilarity, and variance partitioning for this analysis. Fire intensity accounted for a relatively small proportion of variation in alpha and beta diversity, while elevation was the most important predictor. Our results also reveal the important role of the endemic *Lotus campylocladus* ssp. *hillebrandii* (Christ) Sandral & D.D.Sokoloff for understory diversity after fire. Its dominance likely reduces the ability of other species to establish by taking up nutrients and water and by shading the ground. The mid- to long-term effects are unclear since *Lotus* is an important nitrogen fixer in *P. canariensis* forests and can reduce post-fire soil erosion on steep slopes.

Keywords: beta diversity; disturbance; ecosystem functioning; fire; island ecology; *Lotus campylocladus* ssp. *hillebrandii*; pine forest; *Pinus canariensis*; Sentinel-2; succession; understory

1. Introduction

Fires influence the environment on several levels. On a global scale, they influence the carbon cycle and the climate [1] and shift the distribution of several biomes [2–4]. On a landscape level, they lead to a mosaic of unburned and burned patches [5,6], with different levels of recovery ability and resilience to fire [7]. On a local level, the burn severity has a long-lasting influence on understory recovery due to soil heating effects [8], soil properties and organisms [9], and nutrient availability [10]. Forests are often well adapted to fire and are able to recover from fire through different mechanisms, e.g., seedling establishment [11–14], resprouting [15], or a mix of several fire adaptations [16]. On oceanic islands with pronounced topography due to volcanic activity, wildfires that are caused by lightning storms or volcanic eruptions are frequent events in terms of evolutionary time scales. Particularly, in forests that accumulate biomass in layers of litter (fuel) and naturally undergo dry periods, ignitions can translate into wildfires. Considering the spatial and ecological isolation of oceanic islands, adaptations to these impacts are to be expected, and non-adapted species establishing in such systems may be regularly eradicated. Although seemingly paradoxical from a human perspective, the casual occurrence of wildfires is known to preserve the functioning and diversity of fire-adapted ecosystems in the long term [17,18].

Fires have important long-term effects beyond the selection of specific plant functional traits. Nutrient cycles are controlled by fires through the mineralization of elements stored in the litter and biomass, often resulting in the mid-term increase of biomass in the understory compared to the pre-fire period [19]. Consequently, fire-prone forest ecosystems can be seen as complex and adaptive systems [20], wherein biotic and abiotic processes interact, and where ecosystem dynamics vary across different spatial and temporal scales. In the natural pine forests of the Canary

Islands, fires have always affected the structure and dynamics of the vegetation, with fire affecting the same area rarely more than once per 20 years [21].

Today, anthropogenic causes of wildfires, whether deliberate or accidental, add to the natural drivers; only a small proportion of the fires on the Canary Islands is now attributed to ignition by natural causes [19,22]. Fire frequency may have been even higher in the last few centuries, when agriculture was the main economic activity. Around the 1960s, fire events changed from more frequent, small-scale fires towards less frequent larger-extent fires [23]. The ambition to suppress fires and avoid economic damage can promote even more severe fires [24,25]. In 2009, a large fire burned about 2000 hectares in the southern part of La Palma. Following a smaller fire in 2012, a large human-induced fire affected 4800 hectares (about 7% of the island's area) in 2016. This last big fire is the subject of this study.

High fire frequency and short time intervals between fires may decrease fire intensity due to the shorter time available for biomass and fuel accumulation. On the downside, lack of vegetation cover due to repeated fires may increase soil erosion on steep slopes [26], reduce water holding and cation exchange capacities, and promote the leaching of nutrients [10,27,28]. The availability of nitrogen peaks shortly after the fire, then decreases [29]. Both nitrogen concentration and mineralization have been shown to decrease for more than 17 years after a fire in forest soils compared to unburned sites [30,31]. Phosphorus levels in the soil initially decrease but recover over time [29]. Due to their strong impact on the pine ecosystems of La Palma, wildfires can homogenize spatial variability of soil parameters and, consequently, also homogenize vegetation patterns [32].

In most ecosystems, the severity and size of fires depend on both the availability of fuel and its state (humidity). In Mediterranean areas, the fuel state, as measured by indices such as SPI or SPEI, controls the burned area [33]. As climate changes, an additional increase in the fire frequency and intensity is expected, especially during periods of drought, but also in consequence of increased biomass accumulation after humid periods [33–37]. The combination of climate warming and drought might even exceed the capacity of forest ecosystems to regenerate after a fire event. The Canary Islands, in their matrix of a subtropical ocean, are expected to experience decreasing amounts of precipitation in the face of climate change [38], possibly leading to an increased fire risk.

The Canary Pine forest ecosystem differs from many other fire-prone forest types. *P. canariensis* is well adapted to frequent and intense wildfires [22]. It has thick, protective bark, serotinous cones and readily re-sprouts from all above-ground organs and roots after fire. Fallen needles accumulate on branches to form thick cushions and on the forest floor to form thick layers, promoting the likelihood of fire outbreaks [19]. *P. canariensis* indirectly benefits from forest fires, as these can eliminate many encroaching shrubs in the understory, while *P. canariensis* likely survives the fire. Otto et al. [11] found that high-intensity fires also halt the seedling establishment of *P. canariensis* shortly after the fire, probably due to a mix of seed bank destruction and unfavorable soil conditions. However, this does not stop the long-term recovery of *P. canariensis* forests. Even severely damaged trees can survive and re-sprout almost immediately. Additionally, seed dispersal from less affected areas supports recovery after a short-term decline in nutrient availability [12]. The species is also well adapted to the overall decrease in precipitation expected for the Canary Islands in the coming decades [39–41].

Island ecosystems are often relatively species-poor due to effective filters for dispersal and immigration [42]. This applies to the Canary Islands, despite their high levels of endemism [43]. The pine forest is characterized by monodominant stands of *P. canariensis*, whose global distribution is limited to the archipelago. *P. canariensis* forests play a key role in maintaining the water balance of several of the Canary Islands. In the canopies of these pine trees, the moisture from clouds condenses on their long pine needles, significantly increasing the total precipitation inside the forest on the windward eastern slopes [22]. Due to the constant trade winds being blocked by the island’s topography, this cloud contact is very frequent.

These forests tend to have low herbaceous species richness, at least in forbs and perennial herbs in the understory. As a general phenomenon, crown fires are known to diversify the patch mosaic of forests in response to site conditions of the terrain [6]. Fire has been found to promote local species richness in burned areas on La Palma [44], while possibly working as a filter for species invasion. The post-fire species assemblage largely reflects the local pre-fire species pool [45]. Some perennial native species are well adapted to fire [46]. Annuals, whose seeds survive fire impact in low intensity crown fires, often emerge after fire.

Vegetation responses after fire depend on fire severity. While severe fires in Canary Island pine forests may result in a complete loss of understory regeneration due to a destroyed seedbank, intermediate fire intensity typically leads to re-emerging plant communities and can even favor pine regeneration [11]. Overall, fires in pine forests may therefore lead to a complex mosaic of species diversity in the understory, depending on fire intensity. However, our understanding of fire-induced ecosystem dynamics, and related nutrient cycles, is limited for these forests.

One species obviously benefiting from fire is *Lotus campylocladus* Webb & Berthel. Its subspecies *hillebrandii* (Christ) Sandral & D.D.Sokoloff. is endemic to La Palma, and the species is endemic to the Canaries, with *Lotus campylocladus* in Tenerife and *Lotus spartioides* Webb & Berthel. in Gran Canaria performing a similar ecological role in the pine forests of those islands. Its seeds can remain dormant for years in layers of non-absorptive pine litter until these are removed through fire, and a topsoil with mineralized nutrients emerges. Then, the rapid growth and flowering of *L. campylocladus* ssp. *hillebrandii* can be triggered by precipitation and increased light availability. Due to its rhizobia’s nitrogen fixing capacity, this dynamic is likely to contribute positively to the nutrient cycling of Canarian pine ecosystems, as fires can also cause losses of soil nitrogen [30]. Thus, after fires, herbaceous species (with readily decomposable biomass) typically emerge for short periods, often at high abundance; the interaction of fire with *P. canariensis* and *L. campylocladus* ssp. *hillebrandii* may be a major factor controlling biodiversity patterns in these forests.

Here, we combine remote sensing with field research to investigate the effects of the large 2016 fire on plant species richness (alpha diversity) and compositional dissimilarity (beta diversity) of pine forest understory on La Palma. A better understanding of the spatio-temporal processes associated with wildfires in Canarian Pine ecosystems is important for managing biodiversity, ecosystem functioning, and the important services provided by these forests.

This study is based on the following hypotheses and expectations that are derived from the strong link between fire intensity and understory species diversity outlined above, given that our field sampling was done 1.5 years after the fire event:

(A) We hypothesized that the highest levels of species alpha and beta diversity would be at intermediate fire intensity;

(B) Lowest abundance of *L. campylocladus* ssp. *hillebrandii* is expected at intermediate fire intensities because of the persisting dominance of *P. canariensis* at low fire intensities and the damage to the seedbank, unfavorable soil conditions, and erosion at high intensities;

(C) As this legume (Lotus) contributes to N-fixing and nutrient availability, we expect an interaction between fire intensity and legume biomass in the effect on biodiversity patterns.

2. Materials and Methods

2.1. Study Area

The Canary Islands are situated offshore of the northwestern African coast in the Atlantic Ocean and are entirely of volcanic origin. La Palma is at the extreme northwest of the archipelago. It is the second-youngest island with an area of 706 km2 [47] and a maximum elevation of 2426 m a.s.l.—the second-highest island. The climate of the island is characterized by dry summers and high solar radiation in the areas not influenced by the trade-wind clouds [48]. Trade winds from the northeast dominate the precipitation pattern, resulting in large differences in precipitation within islands. This also affects the occurrence of *P. canariensis*, which can be found across most of the elevational range of the island, excluding the coastal area [49]. Due to its ability to filter water from moist air, it can survive in areas with as little as 250 mm of rainfall per year, and up to subtropical cloud forests receiving more than 600 mm of rainfall annually [22], with more than 1000 mm at the upper northeastern slopes of the island [48].

Our study area is located on the western slope of the Cumbre Vieja, the youngest part of La Palma (Figure 1), and still volcanically active. Indeed, part of the area has since been subject to the 2021 volcanic eruptions, which started on 19th September after more than 22,000 earthquakes within a week. The investigated region is dissected by a nonpublic dirt road running from north to south, used by the forestry management authorities.

2.2 Remote Sensing

The Sentinel-2 constellation is extremely useful for fire mapping, with a spatial resolution of approx. 10 m and a revisit time of 5 days [50,51]. These sensors have already been used to efficiently map burn severity based on vegetation indices [52–54]. Chen et al. [55] showed high agreement between the normalized difference vegetation index (NDVI) calculated for Landsat scenes and burn severity sampled on the ground. MODIS fire products are also widely used to map fire occurrences, as they offer the advantage of two decades of times series [56–58]. However, they suffer from low spatial resolution (250 m to 1 km).

To assess the fire intensity of the August 2016 fire, two Sentinel-2 scenes before (18 July 2016) and after (17 August 2016) the fire were selected. Due to the resilience of *P. canariensis* to fire damage, tree mortality observed in the field was very low. Therefore, we opted to use remotely sensed fire intensity as a statistically more robust measure. Both scenes were preprocessed to Level-2 analysis-ready data (ARD) using FORCE version 3.5.2 [59]. A monthly composite Landsat 8 near infra-red (NIR) base image was created using images from 2015 to 2020 and used for co-registering the Sentinel-2 scenes to correct for shifts between images and better align pixels. A LiDAR-based digital elevation model from the Cabildo Insular de La Palma with 2 m spatial resolution was used for topographic correction.

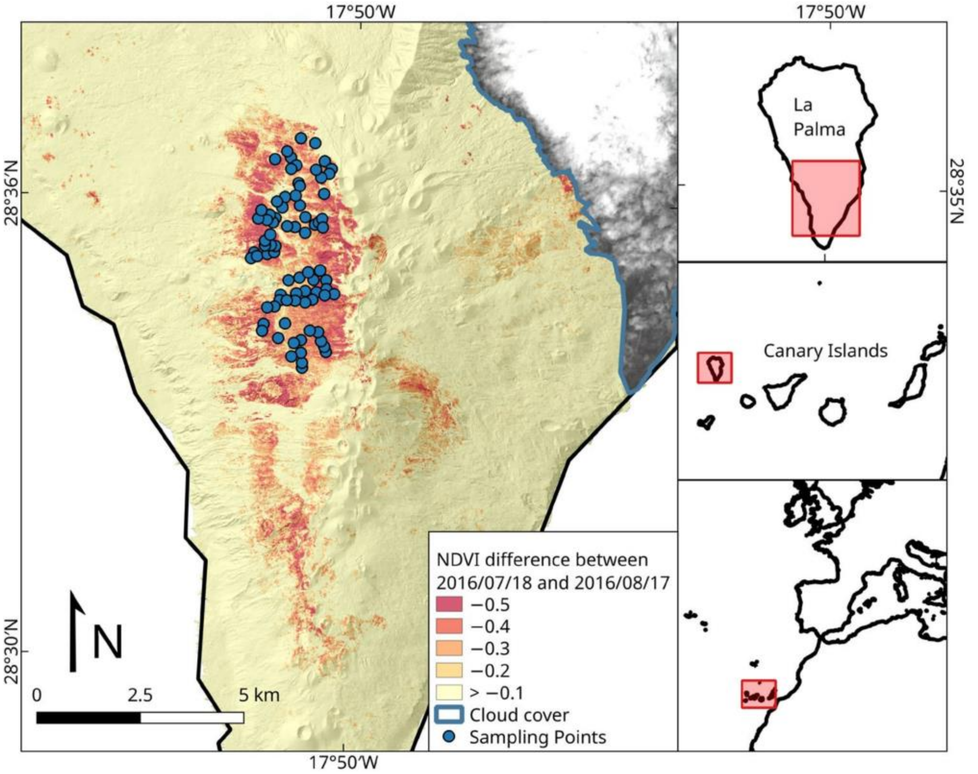

Figure 1. Changes in the Normalized Difference Vegetation Index (NDVI) on the western slopes of the Cumbre Vieja due to a fire in August 2016. The NDVI difference was calculated from two Sentinel-2 images from 18 July to 17 August 2016. The sampling sites of this study are marked with blue dots. The NDVI change in the upper right corner was caused by clouds and therefore masked out.

The NDVI was calculated for both scenes using the following Equation (1):

$$\text{NDVI} = \frac{(\text{NIR} - \text{red})}{(\text{NIR} + \text{red})} = \frac{(\text{Band 8} - \text{Band 4})}{(\text{Band 8} + \text{Band 4})} \tag{1}$$

A NDVI difference map (from now denoted "ΔNDVI") was created by subtracting the NDVI before the fire from the NDVI after the fire. Changes due to the presence of clouds were cropped with a cloud mask. We used the ΔNDVI as a proxy (an inverse one) for fire intensity (Figure 1). For each sampling point, ΔNDVI was extracted using the package "rgdal" 1.5–23 [60] and "raster" version 3.4–5 [61], in R version 3.6.3 [62]. While both Sentinel-2 images were well aligned after co-registration, possible GPS inaccuracies could cause shifts between field measurements and remotely sensed data. Therefore, the mean ΔNDVI was extracted for three buffers with 30, 50 and 100 m radius. Buffers can reveal different landscape patterns, depending on size [63]. The 30 m and 100 m buffer correlated strongly with the NDVI difference value extracted directly at the nearest pixel of the sampling site. The 50 m buffer values only had a Pearson correlation coefficient of 0.65 with the pixel values. Due to the overall good accuracy of the used GPS device of roughly 3 m, it was decided to use the 30 m buffer.

Other spectral indices were also evaluated. The Burned area index (BAI) [64], was overly sensitive to the dark volcanic soils of La Palma and severely overestimated burned area. The Normalized burn ratio (NBR) and its difference, ΔNBR [65], performed reasonably well but decreased the spatial resolution of the output to 20 m due to the use of band 12. ΔNBR had a Pearson correlation of 0.84 with ΔNDVI. Therefore, ΔNDVI was preferred due to its finer spatial resolution.

The Copernicus Tree cover density product for the year 2015 [66] was included as an explanatory variable for canopy cover before the fire. To avoid confusion with the field-measured canopy cover, we refer to the remotely sensed product from before the fire as “Tree cover (RS)” and to the field-measured canopy cover as “Tree cover (field)”.

The Topographic complexity index (TCI) [67] and the Terrain ruggedness index (TRI) [68] were calculated from a 2 m × 2 m resolution DEM provided by the Cabildo Insular de La Palma and was included as measures for local heterogeneity of the topography. The Topographic complexity index represents the ratio between the 3D and 2D surface area (Equation (2))

$$\mathrm{TCI} = \frac{\sum_{100\times 100\mathrm{m}} \left(\frac{\mathrm{Area}_{2\mathrm{m}\times 2\mathrm{m}}}{\cos\left(\mathrm{Slope}_{2\mathrm{m}\times 2\mathrm{m}}\right)} \right)}{\mathrm{Area}_{100\mathrm{m}\times 100\mathrm{m}}} \tag{2}$$

Area2m×2m and Slope2m×2m were calculated per grid cell for a 2 m × 2 m digital elevation model (DEM). Area100m×100m represents a grid cell from a 100 m × 100 m DEM and contains all 2500 2 m × 2 m grid cells. The Terrain ruggedness index quantifies the heterogeneity of terrain with the following Equation (3):

$$\mathrm{TRI} = \sqrt{\sum \left(\mathrm{Elevation}_{\mathrm{ij}} - \mathrm{Elevation}_{00}\right)^2} \tag{3}$$

where $\mathrm{Elevation}_{00}$ is the center cell the TRI is calculated for and $\mathrm{Elevation}_{\mathrm{ij}}$ represents the elevation of the eight neighboring cells.

2.3 Field Sampling and Other Explanatory Variables

Plots were positioned in the burned area of the Canary pine forest on the western slope of Cumbre Vieja. Sampling was done between elevations of 1028 and 1682 m a.s.l. The sampling was focused on the northern part of the burned area (see Figure 1), which was the largest continuous area affected by fire.

Although very steep, inaccessible terrain with barrancos (ravines), and many small-scale forest gaps ruled out a fully random distribution of sampling sites; care was taken to sample evenly over the whole gradient of ΔNDVI. Sampling was conducted in March 2018, in a total of 79 plots. Plot size was 10 m × 10 m because this size matches the spatial resolution of Sentinel-2 and is a standard size applied in forest understory vegetation studies.

All vascular plant species within these plots were recorded, including their estimated cover. Cover values were recorded in percent, with values of 0.0001%, 0.001%, 0.01%, 0.1%, 0.5%, 1%, 2%, 3%, and 5% corresponding to 1 cm^2, 10 cm^2, 100 cm^2, and so on. Values above 5% were estimated and rounded to the nearest 5%. In total, 80 plant species were recorded, with species names following the FloCan checklist [43] (see Figure S1 from Supplementary Materials for an overview of recorded species numbers per site). Additional variables (see Table 1) were recorded for later analysis. Positioning was done with a Garmin Montana 650 GPS device with an accuracy of 3 m.

Table 1. Measured environmental variables. Cover values were estimated for all species within each plot. Additionally, Canopy cover, Shrub cover, Herb cover, and Rock cover were estimated. Basal area was measured using angle count sampling [69]. Diameter at breast height (DBH) was measured for ten trees within the plot. Aspect and Inclination were recorded using a compass with an inclinometer. Aspect was also converted from degrees to both ‘Northness’ and ‘Eastness’ which

were calculated by applying the cosine and the sine function respectively to the measured aspect. Litter depth was calculated by pushing a thin metal rod into the litter until soil or bedrock was hit. Litter depth was measured at four random points within the plot. For both DBH and Litter depth, a mean value and the standard deviation of all measurements were calculated for use in the statistical analysis.

Category	Variable	Unit	Source
Vegetation	Species cover	%	Field measurement
	Herb/shrub cover estimates	%	Field measurement
	Canopy cover	%	Field measurement
	Litter depth	cm	Field measurement
	Basal area	m^2/ha	Field measurement
	Diameter at breast height (DBH)	cm	Field measurement
Topography	Rock cover	%	Field measurement
	Inclination	%	Field measurement
	Elevation	m	Cabildo Insular DEM (2m resolution)
	Aspect	Northness and Eastness	Field measurement, converted with the cosine and sine function

2.4. Statistical Analysis

All statistical analyses were conducted using R version 3.6.3 [62]. Inter-variable correlation was calculated and visualized using package "corrplot" version 0.84 [70] (Figure S2 in Supplementary Materials). This was then used to identify variables with high collinearity (Pearson correlation coefficient above 0.7 or below −0.7) to select the most appropriate one.

To find the best-fitting transformation for all variables, exploratory linear models of the formula species richness ~ x were built, with x representing each variable. Additionally, the transformations x^2, $x + x^2$, sqrt (x) and log (x) were tested. The best transformation was selected based on the AIC of the models. Then, GLMs using family "poisson", and therefore a logarithmic link function, were used to investigate the relationship between species richness and the explanatory variables. The GLM fit was tested using the Chi-square test on residual deviance and degrees of freedom. In addition to two simple GLMs, modelling species richness as functions of elevation and ΔNDVI, respectively, a multivariate model with the selected variable transformations was built. Stepwise variable selection was performed using the "step" function in R to pick the best-fitting GLM. Nagelkerke's pseudo-R2 was calculated for all models, using the "pseudoR2" function from package "DescTools" version 0.99.40 [71].

To test for spatial autocorrelation, Moran's I was calculated for the residuals of each GLM using function "moran.test" from the "spdep" package, version 1.1–5 [72]. For this, a weighted neighborhood matrix was used, which was calculated with the functions "dnearneigh" and "nb2listw", again from the package "sdped". Since significant spatial autocorrelation was found for all GLM residuals, the same analysis was repeated using Spatial linear models (SLM), namely simultaneous autoregressive models (SAR) using the package "spatialreg" version 1.1–5 [73]. SARs are able to account for spatial autocorrelation [74] and are frequently used in Ecology (e.g., [75–77]). The SAR models confirmed the general findings of the GLMs, while accounting for less of the variation in species richness due to the removal of spatial autocorrelation. The results of the SAR models can be found in Table S1 in the Supplementary Materials.

To analyze the influence of both fire intensity and environmental variables on species composition, a distance-based redundancy analysis (dbRDA) [78], using Bray–Curtis dissimilarity, was chosen [79]. Bray–Curtis dissimilarity [80] makes use of the estimated species abundances instead of only using presence–absence data. A dbRDA allows use of other dissimilarity indices apart from Euclidean distance, which is not appropriate for beta diversity analysis without data transformation [81]. Before fitting them to the dbRDA, environmental variables were standardized using the function "decostand" and the method "standardize". After the dbRDA, an ANOVA-like permutation test was performed using the function "anova.cca" from the "vegan" package [82] to assess the significance of environmental variables.

To disentangle the importance of different variables on beta diversity, Mantel tests were performed on four different distance matrices. The environmental distance between each plot and all other plots was calculated using the same variables as the multivariate GLM, with the function "envdist". In the same way, Bray–Curtis dissimilarity, topographic distance (following the surface of the DEM, calculated with the function "topodist" from package "topoDistance" version 1.01 [83]), and ΔΔNDVI were each calculated between every site and all other sites. While the simple difference (ΔNDVI) is used as a proxy for fire intensity per plot, ΔΔNDVI represents the difference between fire intensities between plots. ΔΔNDVI between a sampling site with high ΔNDVI and one with low ΔNDVI would therefore be bigger than between two sites of similar ΔNDVI levels.

Variance partitioning was performed using the function "varpart" to investigate the contribution of fire intensity and topography to the variance in the Bray–Curtis dissimilarity between plots. The following variables were used for topography: Elevation + Elevation^2 + Inclination + Northness + Eastness + TCI + TRI. To further investigate the explanatory power of environmental variables, a permutational MANOVA [84] was calculated using the function "adonis" from package "vegan" with 1000 permutations. *L. campylocladus* ssp. *hillebrandii* poses a challenge for variance partitioning and statistical analyses. On the one hand, Lotus is part of the species pool and therefore influenced by fire intensity and environmental variables in the same way as all other species. On the other hand, the cover of the species in many of our plots is so thick that it influences the occurrence of other species by shading and water uptake. *P. canariensis* has a similar role; while it is a part of the species pool, it is the only species forming the tree layer of our sampling sites. Some predictor variables such as Tree cover (RS) and Basal area are entirely due to *P. canariensis* occurrence. To investigate the influence of using two species both as part of the species pool and the environmental variables, variance partitioning and permutational MANOVA were conducted on four different datasets. The whole dataset, the dataset without *P. canariensis*, the dataset without *L. campylocladus* ssp. *hillebrandii*, and the dataset without both. The dataset without both species only contained 77 observations instead of 79, since two plots contained only *P. canariensis* and *L. campylocladus* ssp. *hillebrandii* without any other species present. Additionally, the dbRDA was repeated with *L. campylocladus* ssp. *hillebrandii* cover removed from the environmental variables.

To assess the role of *L. campylocladus* ssp. *hillebrandii* on beta diversity, local contributions to beta diversity (LCBD) [81] were calculated for all plots using the "adespatial" package version 0.3–8. LCBD values represent "the degree of uniqueness of the sampling units in terms of community composition" [85]. Plots were split into two subsets, above and below 10% *L. campylocladus* ssp. *hillebrandii* cover (38 and 41 plots, respectively) to investigate the effect of *L. campylocladus* ssp. *hillebrandii*. A threshold of 10% was chosen owing to the distribution of *L. campylocladus* ssp. *hillebrandii* in the study area. With one data point with 5%, the other 40 points had 2% or less cover, with 28 points at 0%. Apart from seven points in the 15–30% range, at least a third of the remaining 32 data points had more cover, with 24 points above 50%. Even at 15%, we expect the dense growth (Figure 2) and considerable biomass accumulation of *L. campylocladus* ssp. *hillebrandii* to have an influence on nutrient, water, and light availability in large parts of the plot. Therefore, 10% was chosen as a threshold value. A Wilcoxon test was used to check for significant differences in the LCBD and elevation of both subgroups of plots. Additionally, the species contribution to beta diversity (SCBD) was calculated for all recorded species, based on the Hellinger distance. The Hellinger distance downweighs the occurrence of rare species and thus controls for overestimation due to rare species. To differentiate contributions by life strategy and growth form, SCBD values were also separated into contributions from nitrogen fixing species as well as non-nitrogen fixing species, and herbaceous plants were compared to woody plants.

Figure 2. Thick patchy layers of herbaceous *Lotus campylocladus* ssp. *hillebrandii* one year after forest fire on steep slopes in the southern part of La Palma. Burned *Pinus canariensis* trees are re-sprouting from branches and trunks. It will take several years until canopy closure can be reached again (Photo Carl Beierkuhnlein).

3. Results

The species richness of our plots was best explained by elevation. A GLM with the formula Species Richness ~ Elevation + Elevation^2 (Figure 3a) had a Nagelkerke's pseudo-R^2 of 0.81 ($p < 0.001$; Table 2), indicating higher species richness in lower elevations. The influence of fire intensity, as measured by ΔNDVI, was significant but had a lower pseudo-R^2 of 0.33 (Figure 3b, Table 2); the intermediate fire intensities tended to have the lowest species richness. Species richness was also highest in areas with highest forest density before the fire (Figure 3c, Table 2).

Stepwise variable selection of a multi-predictor GLM produce the following model: Species richness ~ Elevation + Elevation^2 + Tree cover (field) + Tree cover (field)^2 + Northness + Eastness + DBH mean + Litter depth mean + ΔNDVI + ΔNDVI^2 + Tree cover (RS). Its pseudo-R^2 was 0.94 (Table 2).

Significant spatial autocorrelation was detected for the residuals of all GLMs. Using SARs instead of GLMs resulted in differences in the pseudo-R^2 values, but otherwise revealed the same patterns as the GLMs (Table S2 in Supplementary Materials).

Results of the Mantel test revealed similar correlations for the Bray–Curtis dissimilarity and the environmental distance and the topographic distance with Mantel's R of 0.352 and 0.312, respectively (Table 3), while ΔΔNDVI only showed a significant relationship with the environmental distance.

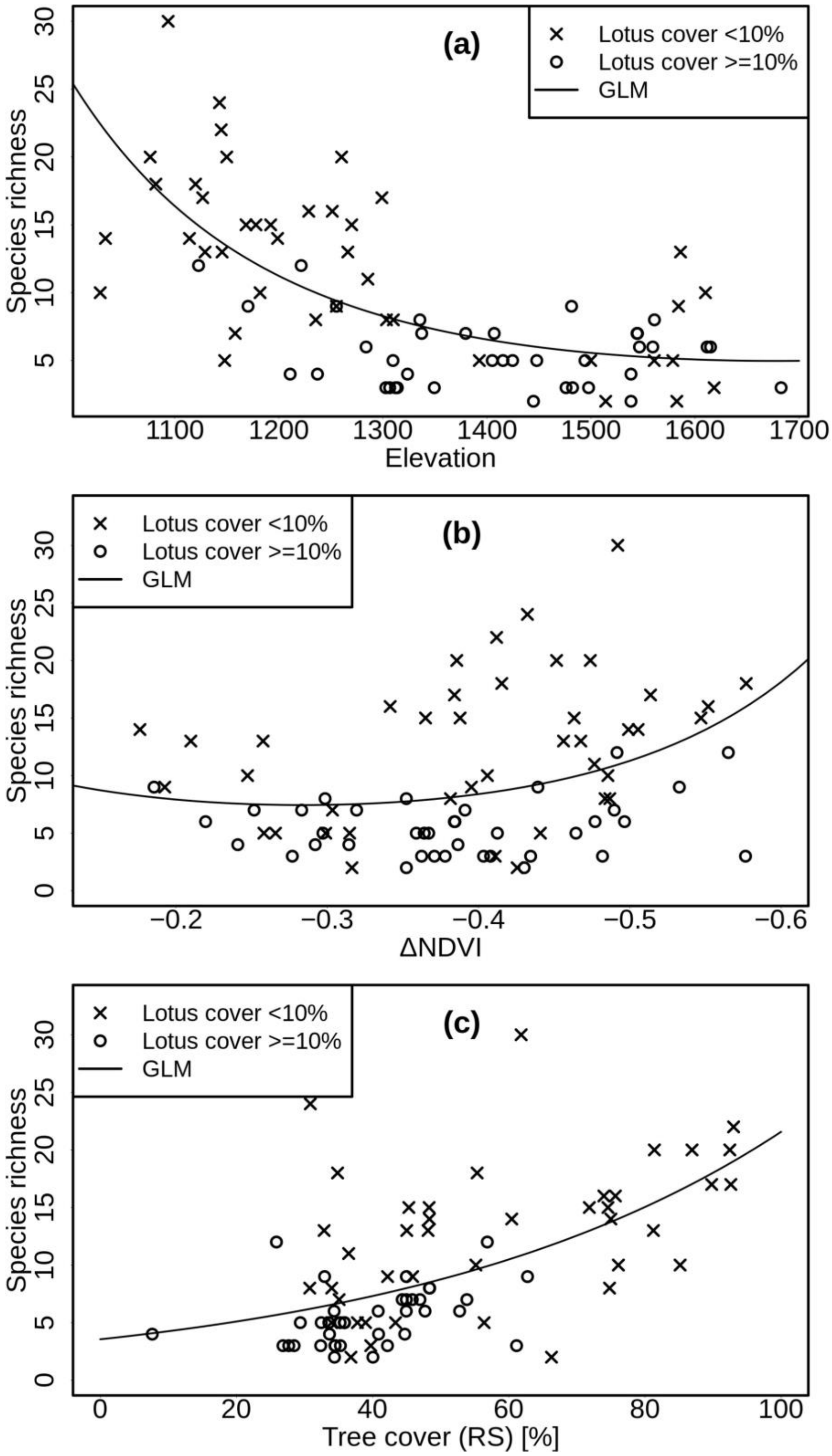

Figure 3. Species richness against (**a**) Elevation (m), (**b**) ΔNDVI, and (**c**) Tree cover (RS) for 79 plots of size 10 m × 10 m. Crosses represent sampling plots with less than 10% *Lotus campylocladus* ssp. *hillebrandii* cover; circles more than 10% cover. The lines represent the fitted GLMs: (**a**) Species richness ~ Elevation + Elevation^2 (Nagelkerke's pseudo-R^2 = 0.81); (**b**) Species richness ~ ΔNDVI + ΔNDVI^2 (pseudo-R^2 = 0.33); (**c**) Species richness ~ Tree cover (RS) (pseudo-R^2 = 0.70). Tree cover (RS) represents the canopy cover before the fire and was extracted from the Copernicus "Tree cover density" product. See Table 2 for more detailed model coefficients.

Table 2. Model coefficients of the different GLMs: species richness modelled first by Elevation + Elevation^2, then by ΔNDVI+ ΔNDVI^2, then by Tree cover from remote sensing, and finally by the multi-predictor GLM Elevation + Elevation^2 + Tree cover (field) + Tree cover (field)^2 + Northness + Eastness + DBH mean + Litter depth mean + ΔNDVI + ΔNDVI^2 + Tree cover (RS). DBH mean is the mean diameter at breast height of ten trees in the plot.

Species Richness~	**Estimate**	**Std. Error**	***z* value**	**Pr (>|*z*|)**	**Significance**
(Intercept)	11.7	2.37	4.92	<0.001	***
Elevation	−0.012	0.00363	−3.3	<0.001	***
Elevation^2	3.57×10^{-6}	1.37×10^{-6}	2.61	0.009	**
R^2 Nagelkerke	0.81		AIC	464.68	
Species richness~	**Estimate**	**Std. Error**	***z* value**	**Pr (>|*z*|)**	
(Intercept)	2.72	0.485	5.62	<0.001	***
ΔNDVI	5.05	2.55	1.98	0.0476	*
ΔNDVI ^{2}	8.9	3.23	2.75	0.0059	**
R^2 Nagelkerke	0.33		AIC	565.9	
Species richness~	**Estimate**	**Std. Error**	***z* value**	**Pr (>|*z*|)**	
(Intercept)	1.27	0.107	11.9	<0.001	***
Tree cover (RS)	0.018	0.00179	10.1	<0.001	***
R^2 Nagelkerke	0.70		AIC	565.9	
Species richness~	**Estimate**	**Std. Error**	***z* value**	**Pr (>|*z*|)**	
(Intercept)	7.63	2.99	2.55	0.0108	*
Elevation	−0.0102	0.00457	−2.23	0.0255	*
Elevation^2	3.02×10^{-6}	1.71×10^{-6}	1.77	0.0763	
Tree cover (field)	0.0101	0.0135	0.746	0.456	
Tree cover (field)^2	−0.000382	0.000201	−1.9	0.0578	
Northness	0.22	0.0844	2.61	0.00898	**
Eastness	−0.166	0.108	−1.54	0.123	
DBH mean	0.0209	0.00677	3.09	0.00202	**
Litter depth mean	0.126	0.047	2.66	0.00774	**
ΔNDVI	−6.2	2.77	−2.24	0.0252	*
ΔNDVI^2	−6.07	3.65	−1.66	0.0963	
Tree cover (RS)	0.00619	0.00226	2.74	0.0062	**
R^2 Nagelkerke	0.935		AIC	400	

The last column marks the level of significance of variables, with *** representing a *p*-value < 0.001, ** below 0.01 and * below 0.05.

Table 3. Mantel test statistic between Bray–Curtis dissimilarity, difference in ΔNDVI between plots ($\Delta\Delta$NDVI), the Topographic distance, and the Euclidian distance between sampling points in terms of their environmental variables. Topographic distance means the "real" distance between datapoints following the surface of a digital elevation model. $\Delta\Delta$NDVI represents the difference between the ΔNDVI values of sampling points and therefore the difference in fire severity between different plots. Numerical values represent the Mantel R. The Mantel test revealed significant correlations (marked by asterisks) between the Bray–Curtis dissimilarity and both the topographic distance and the environmental distance.

	Bray–Curtis Dissimilarity	**$\Delta\Delta$NDVI**	**Topographic Distance**	**Environmental Distance**
Bray–Curtis Dissimilarity	-	0.02	0.31 *	0.35 *
$\Delta\Delta$NDVI	0.02	-	−0.12	0.17 *
Topographic Distance	0.31 *	−0.01	-	0.18 *
Environmental Distance	0.35 *	0.17 *	0.18 *	-

* *p*-value below 0.05.

The dbRDA revealed tree cover (both before and after the fire), elevation and *L. campylocladus* ssp. *hillebrandii* cover percentage as the most influential variables for species composition in our dataset. Plots were separated into two groups based on how abundant *L. campylocladus* ssp. *hillebrandii* was within them. Species were grouped around the center of Axis 1 and Axis 2 with only three species further away from the center: *L. campylocladus, Vicia pubescens* (DC.) Link. and *P. canariensis*. With *Lotus*-cover removed as an explanatory variable, the dbRDA shows a similar pattern, with a higher influence of other species, such as *Bituminaria bituminosa* (L.) C.H.Stirt. and *Chamaecytisus prolifer* (L.f.) Link, both also nitrogen fixers (Figure 4).

A permutational MANOVA revealed that elevation was the most important variable, with Elevation +Elevation^2 explaining between 19.3% (in the subset with *Lotus* only) and 23.4% (in the subset with *Pinus* only) of the variance in the Bray–Curtis dissimilarity (Table S2). Depending on which data subset was used, Tree cover + Tree cover^2 explained up to 24.7% of variance (in the subset with *Pinus* included) and Legume cover + Legume cover^2 explained up to 35.3% (in the subset with both species present).

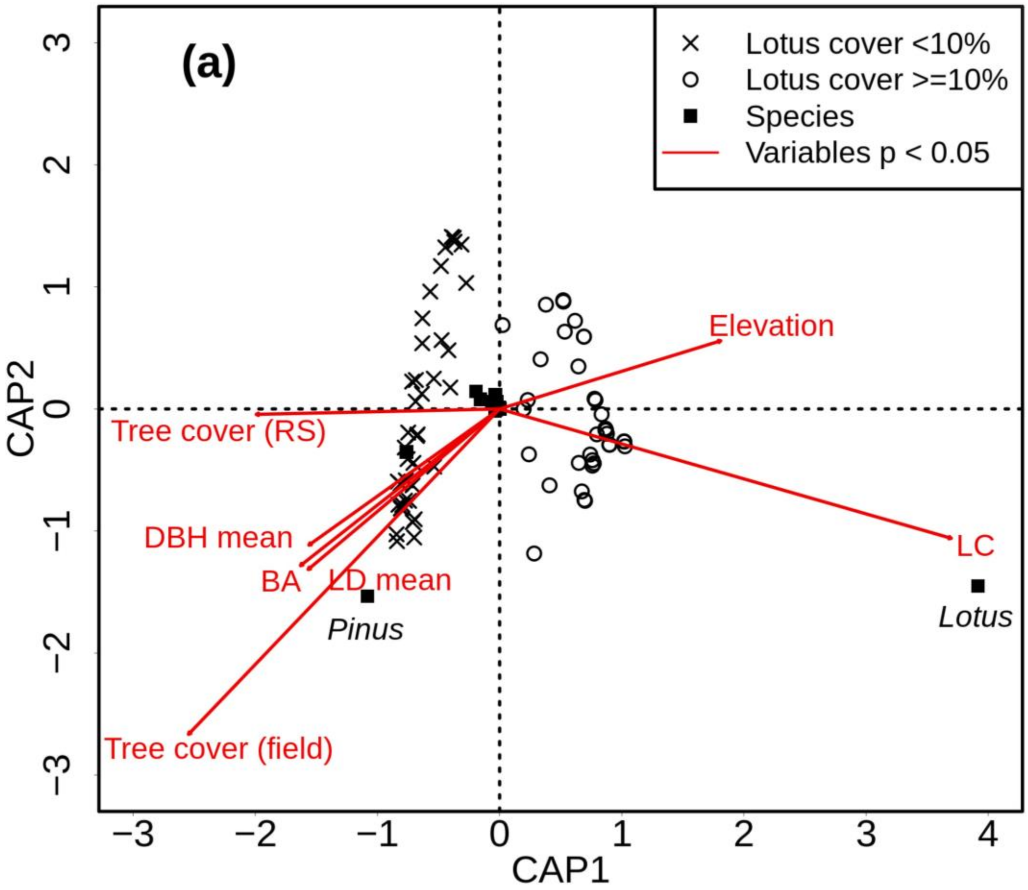

Figure 4. *Cont.*

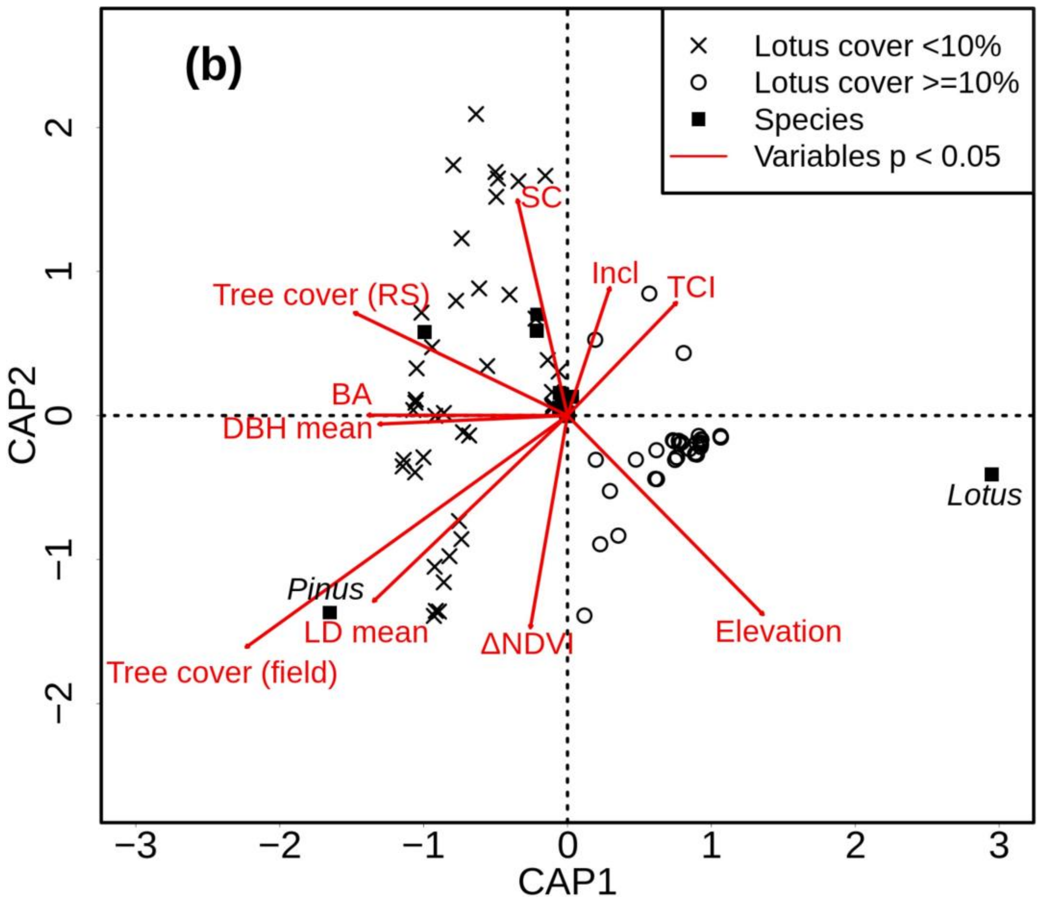

Figure 4. Results of the dbRDA with and without *Lotus campylocladus* ssp. *hillebrandii*: (**a**) includes *Lotus campylocladus* ssp. *hillebrandii* cover both as a species and as an environmental variable. (**b**) excludes *Lotus campylocladus* ssp. *hillebrandii* cover as an environmental variable. Black squares mark distribution of species, which are mostly grouped around the center. Sites are shown as black crosses and circles, with the crosses signifying sites with a *Lotus campylocladus* ssp. *hillebrandii* cover below 10% and circles above 10%. Red arrows represent significant ($p <$ 0.05) environmental variables. Variable names were partially abbreviated for clarity: LC= Lotus cover, SC = Shrub cover, Incl = Inclination, TCI = Topographic complexity index, TRI = Terrain ruggedness index, E = Eastness, N = Northness, LD mean = mean Litter depth, LD sd = standard deviation of Litter depth, DBH mean = mean Diameter at breast height, DBH sd = standard deviation of DBH, CAP1 and CAP2 are the first two constrained axes of the dbRDA. Tree cover (field) is the canopy cover estimated after the fire, Tree cover (RS) is the canopy cover before the fire as derived from the “Tree cover density” product from Copernicus. Non-significant variables were not plotted, to improve clarity. For (**a**), these were ΔNDVI, DBH sd, LD sd, TRI, TCI, Inclination, SC, Northness, and Eastness. For (**b**), these were DBH sd, LD sd, Northness, Eastness, and TRI.

The influence of topography and fire on the Bray–Curtis dissimilarity was tested via variation partitioning. It revealed that topography-related variables account for much more of the variance than ΔNDVI. Topography accounts for between 24.7% of the variance in the subset with only *P. canariensis* included and 20% with both *P. canariensis* and *L. campylocladus* ssp. *hillebrandii* but only 18.4% of the subset without both, and 18.1% in the *L. campylocladus* ssp. *hillebrandii* only subset. ΔNDVI accounts for between 1.7% and 4.3% of the variance are also the most influential in the subset including only *P. canariensis* (Figure 5).

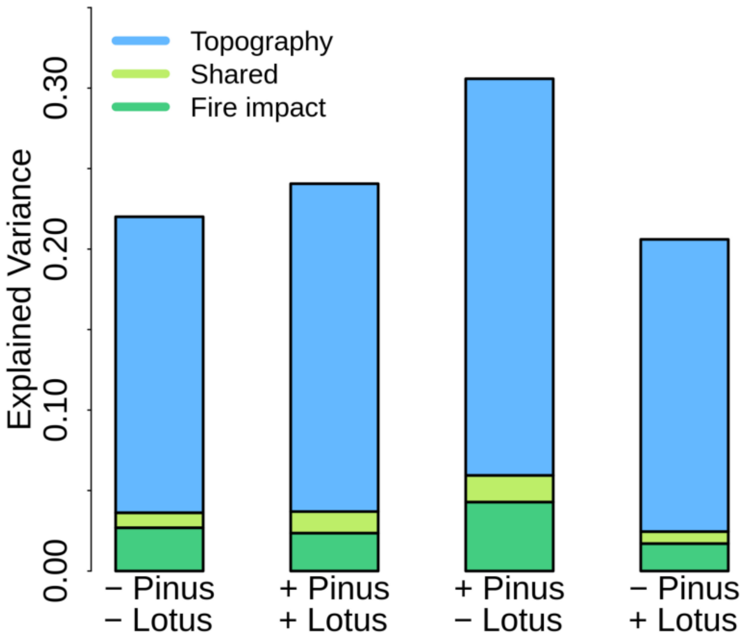

Figure 5. Variance in Canary Island pine forest beta diversity explained by fire impact and topography, tested by variance partitioning. Fire intensity (modelled using ΔNDVI+ΔNDVI^2) and topography (Elevation + Elevation^2 + Inclination + Northness + Eastness + TCI + TRI) are crucial drivers of the Bray–Curtis dissimilarity of plant species across the 79 plots. The community data were split into four subsets: all plant species recorded in the plots, all plant species without *Pinus canariensis*, all plant species without *Lotus campylocladus* ssp. *hillebrandii*, all plant species without *P. canariensis* and *Lotus campylocladus* ssp. *hillebrandii*, because these two species gained dominance in the canopy or in the field layer, respectively. Overall, fire impact accounted for between 1.7% and 4.3% of the variance in Bray–Curtis dissimilarity, and topography from 18.1% to 24.7%. The biggest percentages of explained variance were attained in the data subset including only *P. canariensis*.

Plots dominated by *L. campylocladus* ssp. *hillebrandii* contribute significantly less to local beta diversity. Plots above 10% cover of this species ("*Lotus*-dominated plots") had a mean LCBD value of 0.01, while plots below a 10% cover had a mean value of 0.015 (Figure 6b). Additionally, *Lotus*-dominated plots had significantly lower species richness: a mean of 5.5 compared with 12.5 in the non-*Lotus*-dominated sites (Figure 6a). The distribution of *L. campylocladus* ssp. *hillebrandii* depends on elevation, with *Lotus*- dominated plots being on average 137 m higher than the other sites. All three differences were significant (tested using Wilcoxon tests).

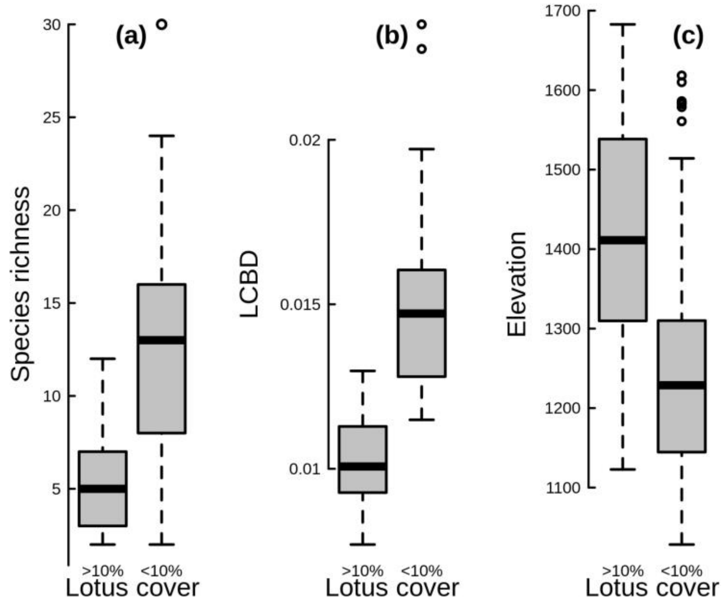

Figure 6. Plots with more than 10% cover of *Lotus campylocladus* ssp. *hillebrandii* (**left**) and below 10% (**right**) and their (**a**) Species richness, (**b**) Local contributions to beta diversity (LCBD), and (**c**) Elevation. All the differences between *Lotus*-cover groups were significant (Wilcoxon test).

Species contributions to beta diversity were tested using the Hellinger distance between plots. *L. campylocladus* ssp. *hillebrandii* was by far the most influential species, SCBD = 0.445, followed by *Vicia pubescens* (0.166), *P. canariensis* (0.115), *Bituminaria bituminosa* (0.063), *Chamaecytisus proliferus* (0.042), and *Cistus symphytifolius* Lam. (0.028) (Figure 6c). Legume species were responsible for 75% of SCBDs, non-legumes for 25%. Herbaceous plants contributed 78% to SCBDs, and woody plants 22% (Figure 7).

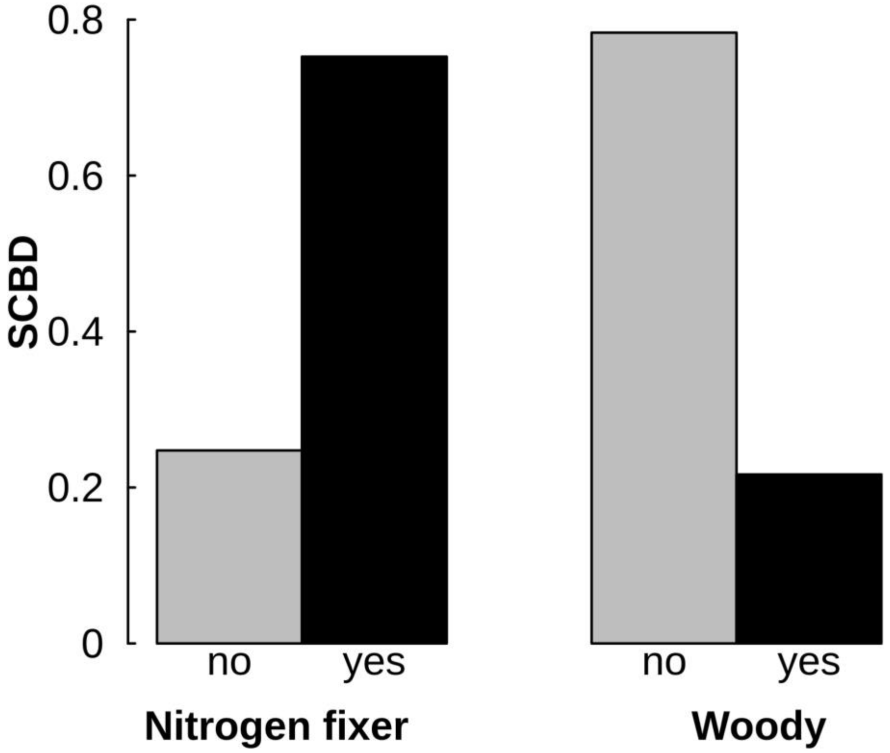

Figure 7. Species contributions to beta diversity (SCBD) based on Bray–Curtis dissimilarity, grouped by legume species vs. non-legume species (“Nitrogen Fixer”), and herbaceous vs. woody species. Nitrogen-fixing legume species contributed more to local beta diversity than other herbs did. The same is true for herbaceous species compared to woody species. Nitrogen fixing species, while making up only 25% of species, contribute 59.5% of species cover and were responsible for 75% of SCBDs, and non-legumes for 25% of SCBDs. Herbaceous plants (81% of species) contributed 78% to SCBDs while contributing only 61% of cover. Woody plants are responsible for 22% of SCBDs, while making up 19% of species and 39% of species cover.

4. Discussion

This study on forest ecosystem dynamics after fire in the endemic pine forest of La Palma, Canary Islands, identified major drivers of the alpha and beta diversity of vascular plant species. In particular, we found that elevation is not only the most important predictor for species richness, it also strongly affects the beta diversity between plots.

4.1 Alpha Diversity (Species Richness)

The most important predictor for plot-level species richness was elevation, with higher species numbers in lower elevations. Even though the sampling of this study covered a limited altitudinal gradient (654 m), elevation could account for a large proportion of the variation in species richness (pseudo-R^2 of 0.81), as well as temperature and precipitation gradients with elevation, in which rainfall seasonality increases at higher elevations [77]. The lower elevation of the investigated gradient was close to roads and villages, explaining the emergence of ruderal and garden plants. Burned areas are known to be more prone to invasion processes [86]. A study by Steinbauer et al. [87] found a decrease in species richness with increasing altitude due to decreasing area and increasing climatic isolation—which is in line with our findings. Irl et al. [77] found elevation to be the most important predictor for species richness on La Palma; the explanatory power of elevation in our study is even higher. The opening of the forest canopy leads to a more direct influence of climatic factors compared to dense forests. The relatively uniform topography throughout our study area may reduce influences of specific site conditions. Finally, the importance of elevation is inflated by spatial autocorrelation, which is shown by the difference in explained variance between the GLM and the SAR model.

ΔNDVI, which serves as a proxy for fire intensity, also explained part of the variation in species richness (Nagelkerke's pseudo-R^2 = 0.33). Our sampled sites showed strong NDVI declines after the fire. In contrast to our hypothesis, more species were encountered in areas with a large difference in NDVI (high relative fire intensity). This is surprising, as seeds from several endemic plants of the Canary pine forest are known to show low germination rates after fire [88]. However, improved nutrient availability may have led to the highest species richness in areas with the largest ΔNDVI; Durán et al. [29] found a steep increase in the availability of soil nitrogen one year after a fire.

As our study shows, due to their relatively high spectral, spatial, and temporal resolution, Sentinel-2 data are very useful for fire-related applications. They can also be used for wildfire ignition probability modelling [89], fire damage mapping [90,91], with an accuracy comparable to unmanned aerial vehicles (UAVs) [53], and are also efficient for fire recovery mapping [92].

While NDVI and other spectral indices are good proxies for fire intensity on the ground [52,53,55], the stand density of *P. canariensis* could negatively affect the usefulness of vegetation indices as a direct proxy for fire intensity. Large gaps in the forest canopy might influence how well fire intensity is recorded in the satellite image. The mean tree cover before the fire, as derived from Copernicus, was 49%. On the other hand, the tree cover before the fire was quite a good predictor of species richness after the fire. As tree density in undisturbed forests is an indicator of resource availability, this could translate into the successional trajectories after fire.

Studies from pine forests in other biomes have shown different response patterns to those we found [93,94], indicating that the impact of fire intensity and the responses of pine forests to wildfire are context-dependent.

4.2. Beta Diversity

Beta diversity measures differences in community composition and adds another category of information to the assessment of biodiversity responses to disturbances. Multitemporal Sentinel-2 and LiDAR data have been linked successfully to species diversity on slopes in northwestern La Palma, with up to 85% of beta diversity reflected in patterns of remotely sensed data [95].

However, there is a multitude of beta diversity indices, highlighting quite different aspects of community responses [79,81,96–98]. In order to cover these different facets of beta diversity, we selected complementary metrics of beta diversity: the classic Bray–Curtis dissimilarity index, the modern LCBD, and the modern SCBD based on the Hellinger distance.

We found correlations between the species dissimilarity and both topographic distance and environmental distance. Increasing dissimilarity with distance is not surprising, but environmental variables show a correlation of similar strength. Elevation and *L. campylocladus* cover were the most important predictors influencing the compositional dissimilarity between plots, with elevation explaining 19.2–23.4% of the variation, depending on the subset under consideration.

Variance partitioning revealed topography to be of higher importance than fire intensity when explaining beta diversity. The highest explained variance was reached in the dataset that included *Pinus* but excluded *Lotus.* This is most likely due to the more direct effect burn damage has on *P. canariensis* compared to understory vegetation, which only germinates after the fire. Therefore, fire intensity has a higher explanatory power for the *P. canariensis* dataset. Since the severity of fire damage is linked to topographic variables, especially elevation and slope, topography and the shared variance explained by both topography and fire intensity are higher as well. In the future, this link between topographic variables and damage to *P. canariensis* could also be used for fire modelling.

The higher abundance of *L. campylocladus* at higher elevations may cause more homogenous patterns there, with a more heterogenous landscape mosaic at lower elevations. Other significant variables were Tree cover and Legume cover. Both variables explained significant yet minor parts of the variation in the subsets without *Lotus* and *Pinus*. ΔNDVI had a significant influence as well, explaining around 4.1–5.5% of the variation in beta diversity, with the highest values reached in the subset including *Pinus* and excluding *Lotus*. Again, this is not surprising, since *P. canariensis* is directly affected by burn damage, while nearly all the other recorded species germinated after the fire. Fire intensity's effects on beta diversity must be interpreted carefully, due to mechanisms in which species were grouped before the fire due to habitat filtering or dispersal limitations and subsequently "unclumped" due to the niche selection of fire tolerant species and differences in sample sizes [99].

Conducting the PERMANOVA on the data subsets without *Lotus* and without *Pinus* revealed minor shifts in the importance of variables. In the presence of *Lotus*, the importance of elevation as a predictor variable decreased. Variance partitioning also revealed the lower importance of both fire intensity and topography compared to the subsets with *Pinus* included. The subsets with *Pinus* included exhibited more variance explained by fire intensity in both the PERMANOVA and the variance partitioning approach. Again, it can be assumed that this is caused by the much more direct effect fire has on *Pinus* compared to understory vegetation. Elevation also had a larger effect on the subsets with *Pinus* included. With differences in the moisture regime in higher elevations close to the Cumbre Vieja compared to lower regions, the recovery and therefore the cover of *Pinus* after the fire seem to be linked to precipitation.

4.3. Role of Lotus campylocladus ssp. *hillebrandii*

Overall, *L. campylocladus* was found to be an important factor for both alpha and beta diversity. This species was encountered in 52 plots, 39 of which had 15% or more cover and 21 had 70% or more cover. The thick layer of this endemic plant appears to limit overall species richness and homogenize beta diversity. Nonetheless, *L. campylocladus* had the strongest influence on the species' contributions to beta diversity (SCBD).

Lotus campylocladus ssp. *hillebrandii* thrives if a combination of fire and precipitation is provided. The data presented in this study were sampled towards the end of the moist season. Studies during and after the drier summer months could shed more light on species composition during forest recovery.

L. campylocladus can be classified as both a perennial herb and a dwarf shrub [100]. Since *Lotus* is usually a temporal occurrence in our study area and mostly lacked wooden stems, we classified it as herbaceous. With its ability to quickly cover open ground after fire, it hinders erosion and nutrient loss [30]. *L. campylocladus* and other nitrogen fixers are important factors for beta diversity. Four out of five of the highest SCBD values were nitrogen fixers. Generally, herbaceous plants contributed more to SCBD than woody plants.

On undisturbed sites, both nitrogen fixers and annual species reach higher abundances in the pine forests on the western slope of Cumbre Vieja compared to the eastern slope [101]. The low abundances of perennial plants indicate that these are less well adapted to fire impact. However, considering the vegetation structures in unburned Canary pine forests, it seems likely that *Lotus* will be replaced by shrub species in the future. While we found a link between fire intensity and both alpha and beta diversity, this was weaker than expected. Site conditions such as elevation were more important explanatory variables. Moreover, the distribution of *L. campylocladus* ssp. *hillebrandii* was driven mostly by elevation. The expected interaction between the *L. campylocladus* and biodiversity patterns could be confirmed, with the cover of *Lotus* as an important driver for beta diversity patterns.

5. Conclusion

We found a complex mix of drivers to be influencing alpha and beta diversity 1.5 years after a major fire. The most important explanatory environmental variables were related to elevation and to the presence of the key herb *L. campylocladus,* a nitrogen fixing endemic plant species. Elevation was overall the most important driver for both alpha and beta diversity patterns. This importance is most likely caused by a multitude of drivers, for example precipitation patterns changing with elevation. Sampling was conducted after the moist winter season. In this situation, *L. campylocladus* benefits from past fire-related nutrient mineralization and favorable soil water conditions. This combination yields high abundances. The ability of *Lotus* to fix nitrogen might additionally facilitate subsequent successional trajectories.

On a longer timescale, climate change is very likely to further influence the forest vegetation of islands such as La Palma. With the expected increase in both fire frequency and size, and with lessons from past fire recoveries not necessarily holding true for future fires anymore, it is crucial to better understand drivers of forest recovery, both for their importance for local species richness in the rather species poor pine forest, and in terms of the role of understory vegetation in erosion prevention.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/f12121638/s1, Figure S1: Detail map indicating the species richness per site, Figure S2: Correlation table of all variables, Table S1: Model coefficients of the different SAR models taking spatial autocorrelation into account, Table S2: Results of the PERMANOVA with 1000 permutations for the 4 data subsets with and without *Lotus* and *Pinus*.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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Appendix

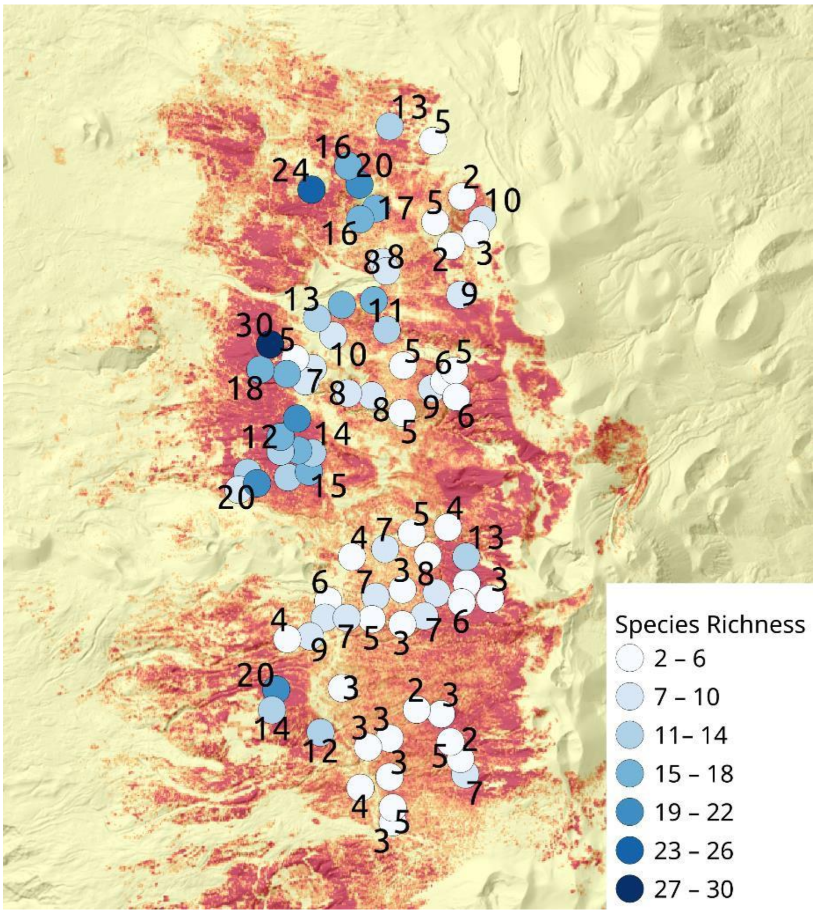
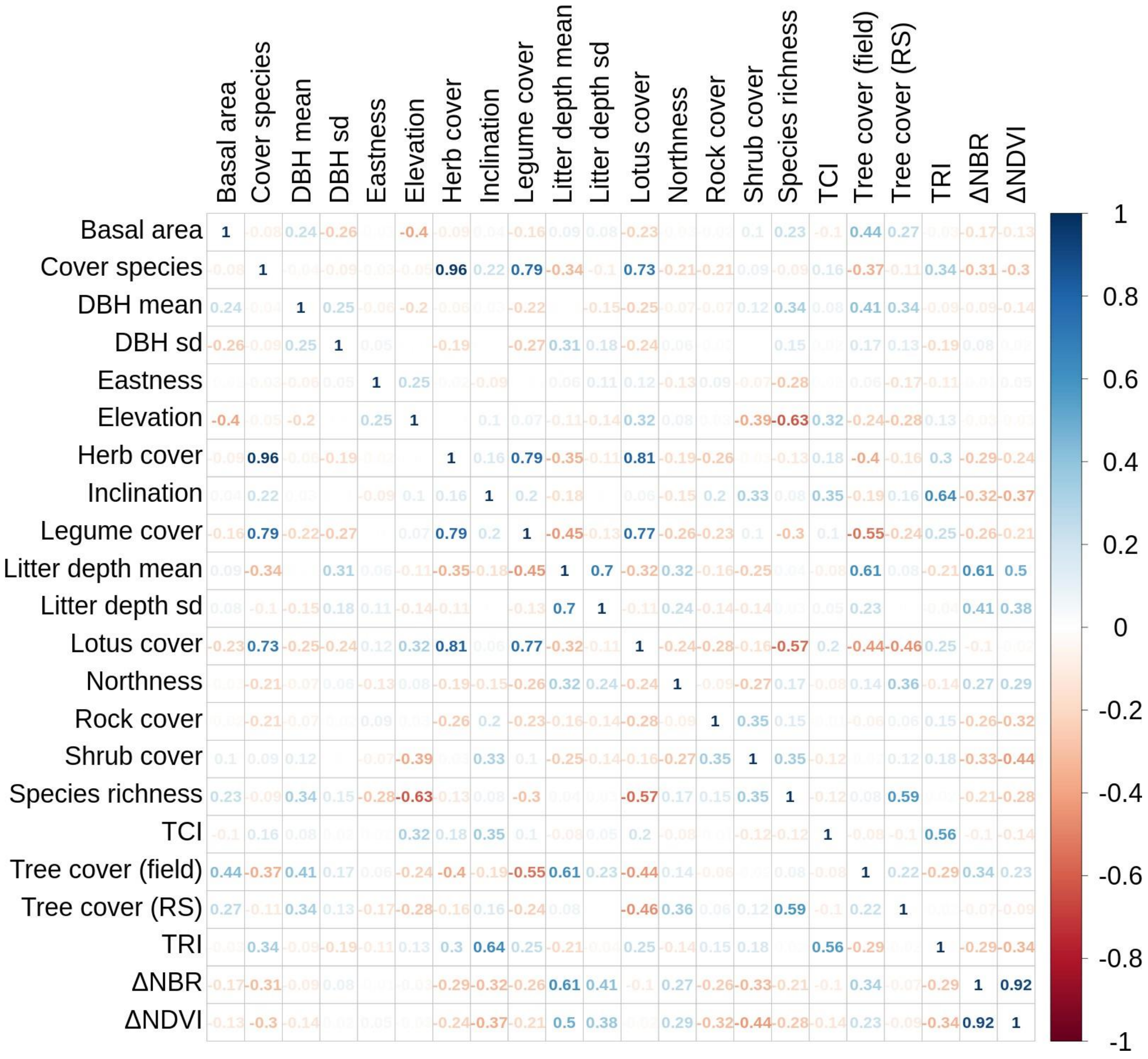


Figure S1. Detail map indicating the species richness per site. Darker blue circles represent more species. The extent of the burnt Canary pine forest is marked in red.



	Basal area	Cover species	DBH mean	DBH sd	Eastness	Elevation	Herb cover	Inclination	Legume cover	Litter depth mean	Litter depth sd	Lotus cover	Northness	Rock cover	Shrub cover	Species richness	TCI	Tree cover (field)	Tree cover (RS)	TRI	ΔNBR	ΔNDVI
Basal area	1	-0.08	0.24	-0.26	0.01	-0.4	-0.09	0.04	-0.16	0.09	0.08	-0.23	0.03	-0.02	0.1	0.23	-0.1	0.44	0.27	-0.03	-0.17	-0.13
Cover species	-0.08	1	-0.04	-0.09	-0.03	-0.05	0.96	0.22	0.79	-0.34	-0.1	0.73	-0.21	-0.21	0.09	-0.09	0.16	-0.37	-0.11	0.34	-0.31	-0.3
DBH mean	0.24	-0.04	1	0.25	-0.06	-0.2	-0.06	0.03	-0.22		-0.15	-0.25	-0.07	-0.07	0.12	0.34	0.08	0.41	0.34	-0.09	-0.09	-0.14
DBH sd	-0.26	-0.09	0.25	1	0.05		-0.19		-0.27	0.31	0.18	-0.24	0.06	0.02		0.15	0.02	0.17	0.13	-0.19	0.08	0.02
Eastness	0.01	-0.03	-0.06	0.05	1	0.25	-0.02	-0.09		0.06	0.11	0.12	-0.13	0.09	-0.07	-0.28	0.02	0.06	-0.17	-0.11	0.01	0.05
Elevation	-0.4	-0.05	-0.2		0.25	1		0.1	0.07	-0.11	-0.14	0.32	0.08	-0.03	-0.39	-0.63	0.32	-0.24	-0.28	0.13	-0.03	-0.03
Herb cover	-0.09	0.96	-0.06	-0.19	-0.02		1	0.16	0.79	-0.35	-0.11	0.81	-0.19	-0.26	0.03	-0.13	0.18	-0.4	-0.16	0.3	-0.29	-0.24
Inclination	0.04	0.22	0.03		-0.09	0.1	0.16	1	0.2	-0.18		0.06	-0.15	0.2	0.33	0.08	0.35	-0.19	0.16	0.64	-0.32	-0.37
Legume cover	-0.16	0.79	-0.22	-0.27		0.07	0.79	0.2	1	-0.45	-0.13	0.77	-0.26	-0.23	0.1	-0.3	0.1	-0.55	-0.24	0.25	-0.26	-0.21
Litter depth mean	0.09	-0.34		0.31	0.06	-0.11	-0.35	-0.18	-0.45	1	0.7	-0.32	0.32	-0.16	-0.25	0.04	-0.08	0.61	0.08	-0.21	0.61	0.5
Litter depth sd	0.08	-0.1	-0.15	0.18	0.11	-0.14	-0.11		-0.13	0.7	1	-0.11	0.24	-0.14	-0.14	0.03	0.05	0.23		-0.04	0.41	0.38
Lotus cover	-0.23	0.73	-0.25	-0.24	0.12	0.32	0.81	0.06	0.77	-0.32	-0.11	1	-0.24	-0.28	-0.16	-0.57	0.2	-0.44	-0.46	0.25	-0.1	0.02
Northness	0.03	-0.21	-0.07	0.06	-0.13	0.08	-0.19	-0.15	-0.26	0.32	0.24	-0.24	1	-0.09	-0.27	0.17	-0.08	0.14	0.36	-0.14	0.27	0.29
Rock cover	-0.02	-0.21	-0.07	0.02	0.09	-0.03	-0.26	0.2	-0.23	-0.16	-0.14	-0.28	-0.09	1	0.35	0.15	0.01	-0.06	0.06	0.15	-0.26	-0.32
Shrub cover	0.1	0.09	0.12		-0.07	-0.39	0.03	0.33	0.1	-0.25	-0.14	-0.16	-0.27	0.35	1	0.35	-0.12	-0.02	0.12	0.18	-0.33	-0.44
Species richness	0.23	-0.09	0.34	0.15	-0.28	-0.63	-0.13	0.08	-0.3	0.04	0.03	-0.57	0.17	0.15	0.35	1	-0.12	0.08	0.59	0.02	-0.21	-0.28
TCI	-0.1	0.16	0.08	0.02	0.02	0.32	0.18	0.35	0.1	-0.08	0.05	0.2	-0.08	0.01	-0.12	-0.12	1	-0.08	-0.1	0.56	-0.1	-0.14
Tree cover (field)	0.44	-0.37	0.41	0.17	0.06	-0.24	-0.4	-0.19	-0.55	0.61	0.23	-0.44	0.14	-0.06	-0.02	0.08	-0.08	1	0.22	-0.29	0.34	0.23
Tree cover (RS)	0.27	-0.11	0.34	0.13	-0.17	-0.28	-0.16	0.16	-0.24	0.08		-0.46	0.36	0.06	0.12	0.59	-0.1	0.22	1	0.02	-0.07	-0.09
TRI	-0.03	0.34	-0.09	-0.19	-0.11	0.13	0.3	0.64	0.25	-0.21	-0.04	0.25	-0.14	0.15	0.18	0.02	0.56	-0.29	0.02	1	-0.29	-0.34
ΔNBR	-0.17	-0.31	-0.09	0.08	0.01	-0.03	-0.29	-0.32	-0.26	0.61	0.41	-0.1	0.27	-0.26	-0.33	-0.21	-0.1	0.34	-0.07	-0.29	1	0.92
ΔNDVI	-0.13	-0.3	-0.14	0.02	0.05	-0.03	-0.24	-0.37	-0.21	0.5	0.38	0.02	0.29	-0.32	-0.44	-0.28	-0.14	0.23	-0.09	-0.34	0.92	1

Figure S2. Correlation table of all variables. DBH sd=standard deviation of the Diameter at breast height; Lotus cover=cover of *Lotus campylocladus* ssp. *hillebrandii*; TCI=Topographic complexity index; TRI= Terrain ruggedness index; ΔNBR=difference in Normalized burn ratio between before and after the fire; ΔNDVI= difference in the Normalized difference vegetation index between before and after the fire.

Table S1. Model coefficients of the different SAR models taking spatial autocorrelation into account. The models use the same variables as the GLMs. While some variables, such as ΔNDVI were not significant the overall models all were. The last table shows a SAR model mimicking the GLM where the explanatory variables were selected by a stepwise algorithm based on AIC. DBH mean is the mean diameter at breast height of ten trees in the plot. The last column marks the level of significance of variables, with *** representing a p-value <0.001, ** below 0.01, * below 0.05 and . below 0.1.

Species richness ~	**Estimate**	**Std. Error**	***z* value**	**Pr($>\lvert z\rvert$)**	**Significance**
(Intercept)	154.67	39.81	3.89	<0.001	***
Elevation	-196.81	59.21	-3.32	<0.001	***
Elevation^2	64.76	2.97	2.97	0.003	**
R^2 Nagelkerke	0.53		AIC	454.67	
Species richness ~	**Estimate**	**Std. Error**	***z* value**	**Pr($>\lvert z\rvert$)**	
(Intercept)	1.08	6.39	0.17	0.87	
ΔNDVI	-28.80	2.55	-0.87	0.38	
ΔNDVI ^{2}	-19.51	3.23	-0.45	0.65	
R^2 Nagelkerke	0.44		AIC	469.63	
Species richness ~	**Estimate**	**Std. Error**	***z* value**	**Pr($>\lvert z\rvert$)**	
(Intercept)	3.13	1.90	1.64	0.09	.
Tree cover (RS)	0.12	0.02	5.36	<0.001	***
R^2 Nagelkerke	0.56		AIC	449.58	
Species richness ~	**Estimate**	**Std. Error**	***z* value**	**Pr($>\lvert z\rvert$)**	
(Intercept)	12.53	7.09	1.77	0.08	.
Elevation	-0.02	0.003	-6.27	<0.001	***
Tree cover (field)	-0.009	0.1	-0.09	0.93	
Tree cover (field)^2	-0. 001	0.001	-1.33	0.18	
Northness	1.81	0.70	2.59	0.009	**
Eastness	-0.61	0.66	-0.93	0.35	
DBH mean	0.14	0. 06	2.38	0.017	*
Litter depth mean	0. 83	0.40	2.05	0.04	*
ΔNDVI	-66.80	24.34	-2.74	0.006	**
ΔNDVI^2	-65.47	31.97	-2.05	0.04	*
Tree cover (RS)	0.09	0.02	4.38	<0.001	***
R^2 Nagelkerke	0.76		AIC	417.94	

Table S2. Results of the PERMANOVA with 1000 permutations for the 4 data subsets: without *Pinus canariensis* and *Lotus campylocladus* ssp. *hillebrandii*, with both, with only *Pinus* and with *only* Lotus. The first columns contain the variables used to explain the Bray–Curtis dissimilarity between plots. DBH stands for the diameter at breast height (DBH), NDVI for the normalized difference vegetation index. The other columns contain the F statistic, the partial R^2 of variables and the p- value. The last column marks the level of significance of variables, with *** representing a p-value <0.001, ** below 0.01, * below 0.05 and . below 0.1.

PERMANOVA	**Species - Pinus - Lotus**				**Species + Pinus + Lotus**			
Bray-Curtis ~.	F Statistic	R^2	Pr(>F)		F Statistic	R^2	Pr(>F)	
Elevation	17.9011	0.1728	<0.001	***	44.7786	0.1492	<0.001	***
Elevation^2	3.3863	0.0327	0.007	**	14.0463	0.0468	<0.001	***
Legume cover	1.9831	0.0191	0.0599	.	91.0426	0.3034	<0.001	***
Legume cover ^{2}	3.8674	0.0373	0.005	**	15.211	0.0507	<0.001	***
Tree cover (field)	2.0653	0.0199	0.047	.	39.3109	0.131	<0.001	***
Tree cover (field)^2	0.6839	0.0066	0.7143		9.2459	0.0308	<0.001	***
Northness	1.167	0.0113	0.2937		1.5538	0.0052	0.1908	
Eastness	1.0799	0.0104	0.3117		0.069	0.0002	0.994	
DBH mean	1.4605	0.0141	0.1469		2.0837	0.0069	0.0909	
Litter depth mean	0.8402	0.0081	0.5085		0.1261	0.0004	0.979	
ΔNDVI	2.5251	0.0244	0.018	*	7.15	0.0238	<0.001	***
ΔNDVI^2	1.7851	0.0172	0.0959		5.9646	0.0199	<0.001	***
Tree cover (RS)	1.8444	0.0178	0.0659	.	4.5211	0.0151	0.01	**
Residuals		0.68				0.22		
	Species + Pinus - Lotus				**Species - Pinus + Lotus**			
	F Statistic	R^2	Pr(>F)		F Statistic	R^2	Pr(>F)	
Elevation	47.9852	0.2062	<0.001	***	23.0612	0.149	<0.001	***
Elevation^2	6.5614	0.0282	<0.001	***	6.6938	0.0433	<0.001	***
Legume cover	24.1923	0.104	<0.001	***	29.6648	0.1917	<0.001	***
Legume cover ^{2}	9.0229	0.0388	<0.001	***	9.0772	0.0587	<0.001	***
Tree cover (field)	44.1869	0.1899	<0.001	***	4.2129	0.0272	0.003	**
Tree cover (field)^2	13.3075	0.0572	<0.001	***	1.7102	0.0111	0.1159	
Northness	2.5053	0.0108	0.045	*	1.0883	0.007	0.3137	
Eastness	1.4398	0.0062	0.2298		0.7729	0.005	0.5574	
DBH mean	1.2082	0.0052	0.2867		1.8156	0.0117	0.0929	
Litter depth mean	0.4138	0.0018	0.8052		0.9515	0.0061	0.4276	
ΔNDVI	7.1457	0.0307	0.002	***	3.8579	0.0249	0.006	**
ΔNDVI^2	5.655	0.0243	0.004	**	3.8351	0.0248	0.006	**
Tree cover (RS)	4.0825	0.0175	0.008	**	3.0059	0.0194	0.018	**
Residuals		0.28				0.42		

6.2 Manuscript 2

SO_2 emission and deposited sulphur at the crater rim of the 2021 Tajogaite eruption

Impact of Volcanic Sulfur Emissions on the Pine Forest of La Palma, Spain

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Authors: Frank Weiser [1,*] , Esther Baumann [1,2], Anke Jentsch [3] , Félix Manuel Medina [4] , Meng Lu [5], Manuel Nogales [6] and Carl Beierkuhnlein [1,7,8]

Affiliations:

[1] Department of Biogeography, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany;

[2] Biomasseinstitut, BIT, University of Applied Sciences, Weihenstephan-Triesdorf, Markgrafenstr. 16, 91746 Weidenbach, Germany

[3] Disturbance Ecology and Vegetation Dynamics, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany;

[4] Consejería de Medio Ambiente, Cabildo Insular de La Palma, 38700 Santa Cruz de La Palma, Spain;

[5] Geoinformatics-Spatial Big Data, University of Bayreuth, Universitätsstr. 30, 95447 Bayreuth, Germany;

[6] Island Ecology and Evolution Research Group, Institute of Natural Products and Agrobiology (IPNA-CSIC), 38206 San Cristóbal de La Laguna, Spain;

[7] Bayreuth Center for Ecology and Environmental Science BayCEER, 95440 Bayreuth, Germany

[8] Geographical Institute Bayreuth, GIB, 95440 Bayreuth, Germany

*** Correspondence**: frank.weiser@uni-bayreuth.de

Abstract

In autumn 2021, the largest volcanic eruption on the island of La Palma in historic records took place. The Canary Islands are of volcanic origin and eruptions have always constituted part of their natural disturbance regime. Until recently, their impacts could not be directly observed and studied. Influence of the emission of phytotoxic gases on biodiversity and ecosystem dynamics was hitherto unknown. The recent eruption is still being intensely monitored. We used Sentinel-2 remote sensing data to analyze the spatial extent and intensity of the impact related to sulfuric emissions, aiming to understand the damage patterns in Canary pine forest. The emissions damaged 10% of that forest and affected 5.3% of the Natura 2000 protected areas. We concluded that this is largely due to the toxic effects of the enormous emissions of SO_2. We found a clear correlation between the change in the normalized difference vegetation index (NDVI) and distance from the eruption. This pattern was weakly anisotropic, with stronger damage in southern directions. Counteracting effects, such as ash deposition, were largely excluded by combining NDVI change detection with tree cover density. We expect that vegetation damage will be transient. *P. canariensis* can resprout after forest fires, where most leaves are lost. Consequently, our assessment can serve as a reference for future ecosystem regeneration.

Keywords: Sentinel-2; natural pollution; chlorosis; natural disturbances; volcanism; oceanic island; sulfur; *Pinus canariensis*; pine forest; Cumbre Vieja; volcanic eruption

1. **Introduction**

Oceanic islands generally receive great attention in terms of nature conservation. Threats to their ecosystems are mostly linked to human impacts, climate change, and invasive introduced species [1,2]. Natural impacts such as volcanic eruptions, landslides, or earthquakes, are known to be important, often resulting in compound disturbances including cascading effects [3], but are widely ignored due to their low frequency and mainly for the fact that they can rarely be monitored directly.

The legacy of volcanic activity has made the Canary Islands an iconic place for volcanology and geology. The term "caldera" (cauldron), for instance, dates back to the description of La Palma and the "Caldera de Taburiente" by Leopold von Buch in 1825 [4], even though he did not correctly understand the local processes. The archipelago has been shaped for more than 20 million years (Ma) by volcanic eruptions. Soil formation, nutrient availability, aquifers and groundwater formation, and surface structures are directly linked to these events and to the duration of weathering processes after volcanic activity ceased. However, transient geochemical processes in the past, such as sulfuric emissions and their historic impact, cannot be traced backwards. Additionally, the linkages between geological processes and ecosystems are often restricted to elevation [5–7] or to the age of historic lava flows [8].

The southern part of the island of La Palma was the arena for a series of volcanic eruptions in historic time periods, with the latest ones in 1949 and 1971. Most of these eruptions and lava flows were on the western slope of the Cumbre Vieja mountain ridge, which is historically the most active volcano on the Canary Islands (eight eruptions between 1500 and 2020) [9]. This 2021 eruption was notably the largest in the historic record in terms of area directly affected by lava flows and the longest in duration. Volcanic unrest began in 2017, with alternating periods of calm and unrest [10,11]. Volcanic unrest increased in magnitude and severity only 8 days before the eruption [12]. Occurring at a location formerly called "Hoya de Tajogaite", it produced huge amounts of lava (covering 1241 ha) and ash (covering 65 km^2). Settlements (2988 buildings) and roads (92.1 km) disappeared under the eruptive materials [13].

Natural and seminatural vegetation, such as pine forest, succulent shrubs, palm groves and coastal vegetation were wiped out. However, the negative impact ranges far beyond the area now directly covered by new volcanic rock. The area affected by deposition of large amounts of volcanic ash (tephra and lapilli) is even larger, but not clearly delineated.

The effects of volcanic gases were the most severe and extensive. Besides CO_2, substantial amounts of SO_2 were released (Figure 1). SO_2 reacts in the atmosphere with water vapor and oxygen to form a toxic haze called "vog" with dispersed sulfuric acid and sulfate aerosols. The effect of SO_2 has been extensively researched, mostly in the context of anthropogenic industrial pollution [14–16], as it has a major influence on the global climate [17]. Effects on plants are complex, as they occur at both an individual and community scale [18], and can act as a general toxin on several levels of plant functioning [19]. While low doses of SO_2 may benefit plants due to its role as an essential nutrient, higher doses can cause extensive damage. SO_2 uptake can hinder the ability of plants to close their stomata, leading to water loss [19]. SO_2 also hinders other plant processes, such as respiration, enzyme activity, and protein synthesis [18], affecting the uptake of CO_2 during photosynthesis [20]. Overall, high SO_2 concentrations can lead to both acute injury of plant parts and chronic injuries, such as chlorosis [19]. Acute damage to pine trees is often visible as brown necrosis, clearly separated from the healthy part of the needles [21]. Both intensities of damage often lead to permanent defoliation [21,22]. In addition to the direct, phototoxic effects of sulfur deposition, there are also indirect effects on forests, such as soil acidification [23,24], water contamination [25], increased availability of heavy metals, and damage to mycorrhizal roots [26].

Volcanic eruptions contribute significantly to global SO_2 emissions. While they account for 7% of global sulfur, they are the source of 18% of sulfur in the atmospheric column [27]. The eruption of Pinatubo in 1991 reached the stratosphere [28], allowing the long-range spread of aerosols. Volcanic emissions from Africa have been measured above the Amazon rain forest [29], and SO_2 from southern Chile reached South Africa [30]. However, due to the mix of anthropogenic, biotic, and volcanic sulfur in the atmosphere, to our knowledge there are few studies on the exact impact of volcanic SO_2 on forests. The same is true for persistent volcanic degassing [31].

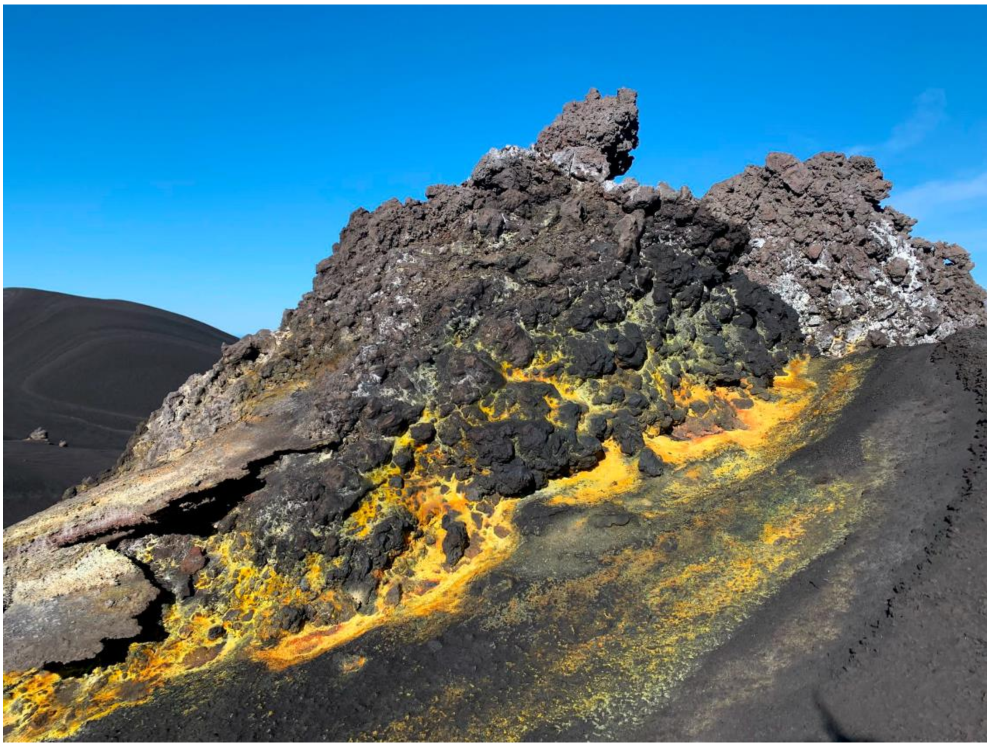


Figure 1. Solfatar elementary sulfur deposits close to the volcanic cone. (Photo: Jorge Parra).

The spread of SO_2 from all sources can be monitored by satellite instruments, such as TROPOMI, which is onboard Sentinel-5P (European Earth Observation program Copernicus) [32]. The TROPOMI measurements indicated total emissions of SO_2 assessed to an amount of approximately 1 Tg of SO_2 [33]. This ranks the eruption within the top 50 SO_2 emissions since satellite measurements yielded quantitative values (1978).

In this study, we scrutinize and trace the impact of sulfuric gases on the unique Canary pine forest. We hypothesize that the huge amount of emitted sulfuric compounds would be reflected in chlorotic changes to the pine canopy and that such impacts may be detected from Earth observations. We furthermore predicted that the predominant wind directions during the individual days of volcanic activity will explain the spatial pattern of vegetation damage related to volcanic gases. As gases are rapidly distributed in different layers of the atmosphere depending on the intensity of volcanic activity, it is evident that the recorded emissions cannot be directly translated into effects on the ground, but rather serve as a rough orientation. However, the amount of emitted sulfur is so high that an influence on terrestrial ecosystems is likely to occur.

2. Study Area

The island of La Palma is one of the westernmost islands of the Canary archipelago (Figure 2), with an area of 708 km^2. Its highest elevation of 2426 m a.s.l. is reached at Roque de los Muchachos. The island is subdivided into an older part with higher elevation in the north, and a younger part in the south. In the northern half of the island, volcanic activity stopped hundreds of thousands of years ago. However, the southern half of the island has continued to be active until today. A total of eight eruptions have taken place in historic times and more than 80 volcanic cones have been perfectly identified. Here, the current volcanic activity also took place. The volcanic eruption on the western slope of Cumbre Vieja (at a location called Hoya de Tajogaite or Cabeza de Vaca) on La Palma began on 19 September and lasted until 13 December 2021. With this duration, the eruption became the longest on this island, based on historical chronicles dating back to the 15th century.

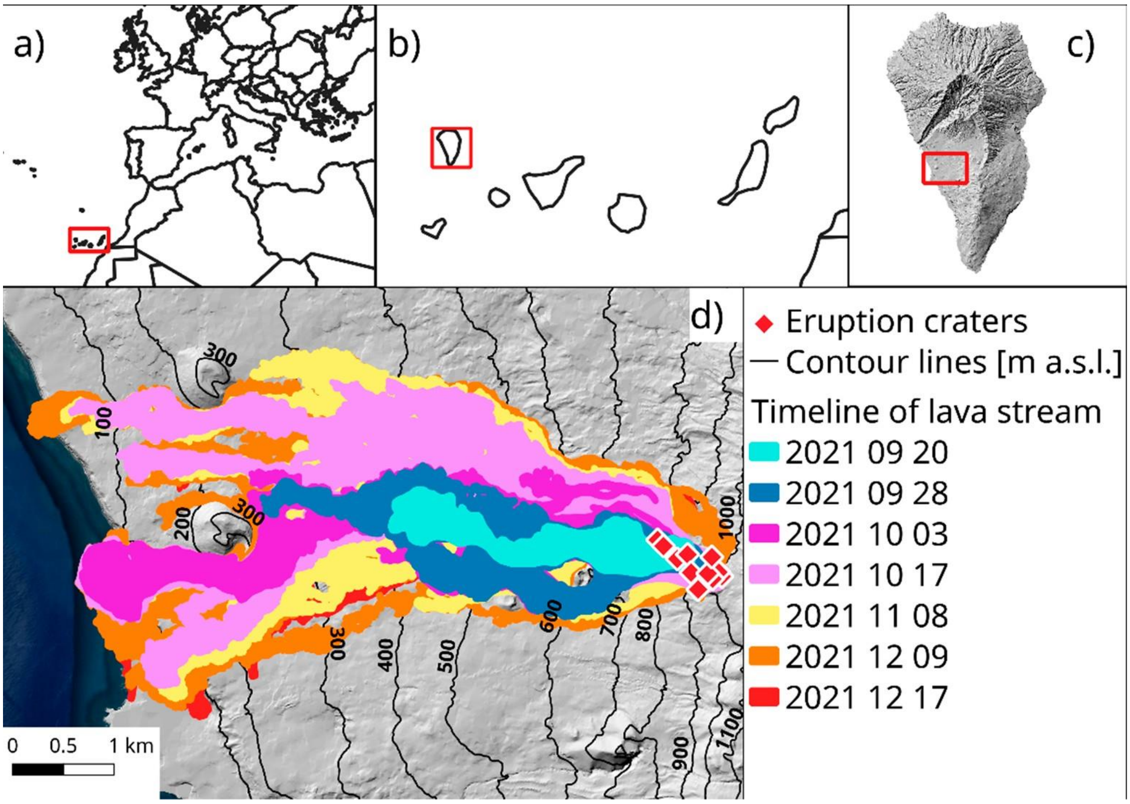


Figure 2. Lava stream resulting from the volcanic eruptions on the island of La Palma, Spain. Location of (**a**) the Canary Islands, (**b**) the island of La Palma, (**c**) location of the eruption and lava flows on the western flank of Cumbre Vieja, (**d**) extent and sequence of lava flows between 19 September and 14 December 2021. Data source for the lava stream is the grading products created by the Copernicus Emergency Management System. The background map in (**c**,**d**) is a hillshade created from a 2 m-resolution digital elevation model provided by the Cabildo Insular de La Palma.

The climate of La Palma is generally subtropical and oceanic with warm temperatures and less pronounced seasonality. Besides the climatic gradients along elevation, the most pronounced differences are evidently related to elevation and aspect [34,35]. The northeast-facing slopes are exposed to trade winds and are regularly covered by clouds condensing on these high mountains. In contrast, the southwest-facing slopes, such as the one with this volcano, are characterized by low cloudiness, arid to semi-arid conditions, and high temperatures, particularly on the bare ground of young volcanic rocks and lapilli (tephra) fields.

La Palma is known as “La Isla Bonita” or “La Isla Verde”, which addresses the lush vegetation that covers its steep slopes due to the favorable moist climate. As accessibility is limited, and human population density is low, a large extent of the island is still covered by natural and semi-natural vegetation, e.g., laurel forest and Morello-*Erica* thickets, particularly in the isolated valleys along the northern coast, and legume shrub vegetation in the alpine zone. Native trees cannot thrive only in the alpine zone above the treeline and in the most arid parts at lower elevations. As human influences related to land use are minor, most of the woodland is mainly characterized by natural disturbance regimes [36,37].

Due to the geographic isolation of individual islands of the Canary archipelago and of their respective ecosystems, all islands host rare, endemic, and endangered plant species [38]. Canary pine forest on La Palma covers 250 km^2, of which 208 km^2 (83%) is within protected areas with restrictions for management and land use. A total of 238 plant species have been recorded for this ecosystem, among which 127 plant species are endemic to the Canaries and the other 44 to only La Palma. Most plant species in this ecosystem (90%) are native. Only a few invasive species are established in this ecosystem characterized by extreme natural disturbances [39]. This high degree of endemicity and naturalness interms of human impact and diverse species assemblages attributes a high value to the Canary pine forest [40]

The Canary pine forest is a major ecosystem in the archipelago [40], which has provided a wide range of ecosystem services, including slope stabilization, timber and pitch production, shedding of needle litter usable as packing material, maintenance of ground freshwater by cloud condensation (horizontal precipitation), and an attraction for tourists and leisure activities. On La Palma, managed plantations are very scarce. Most of its pine forests are dominated by the endemic species *Pinus canariensis* C. Sm., showing natural conifer dynamics. Large parts of these ecosystems are protected as Natura 2000 nature reserves. Canary pine is the largest Old World pine species, reaching up to 60 m in height and more than 2.5 m in diameter at breast height (DBH) [41]. However, such impressive trees are rare due to the massive historical felling and exploitation of pine forests [42]

Canary pine forests are frequently exposed to severe disturbances such as large wildfires, both natural and anthropogenic in origin [43]. Besides the direct impact of fires, nutrient availability in Canary pine forest soils is also affected [44]. However, *P. canariensis* is highly adapted to fire impact [45–48]; it can recover after fire by resprouting from epicormic and root collar buds, shaping a peculiar morphology of fire-impacted trees. The trees survive even intense crown fires. Within a few years, the previous canopy cover can be reached again [49]. The species additionally has very thick bark and a high concentration of carbohydrates in the sapwood parenchyma cells [47,50]. The extremely long needles of this pine aid substantially in freshwater provision [51], by contributing to condensation during the frequent fog (clouds touching the ground). In addition, this ecosystem is naturally rather species-poor. The forest structure and canopy are dominated by *P. canariensis*, while the understory is composed of herb and shrub species. In consequence, damage to the pine tree canopy has a negative influence on the entire ecosystem. In addition, such damage can be seen as an indicator of pollution impact, which may also affect other species that cannot be detected by remote sensing information.

3. Materials and Methods

3.1. Data Collection

To assess chlorotic damage to the Canary pine forest after the recent eruption in 2021, we chose Sentinel-2 satellite images, which are well-suited for detecting different types of forest damage, e.g., fire damage [37,52], drought [53], bark beetle infestations [54], and defoliation [55]. To compare forest conditions before and after the eruption, all Sentinel-2 images between 19 September 2021 and 14 December 2021 were processed. Overall, 30 images from Sentinel-2 military grid reference system (MGRS) tiles T27RYM and T28RBS were evaluated. However, both smoke from the eruption and cloud formation due to aerosols left very few images clear enough to be usable. Therefore, two images were selected for a before-and-after comparison: 30 November 2019, a near-cloud-free image representing conditions before the eruption, and an image from 14 December 2021, which was the first Sentinel-2 image available with cloud cover low enough to analyze chlorotic damage to the forest. All images were downloaded at processing Level 2A and pre-processed with the R package "sen2r" version 1.5 [56]. All pixels with the levels "No data", "Saturated and defective", and "Cloud (high and medium probability)" in the included scene classification layer (SCL) were masked out, with a 200 m buffer around the clouds masked out as well. We also attempted to mask other pixel values, such as those containing thin cirrus clouds. The high aerosol concentration in the atmosphere resulting from volcanic activity (Figure 3) led to us masking most parts of the island. While these aerosols negatively affect image quality if not masked out, the observed chlorosis of the pine forest was severe enough to render these introduced errors negligible. Masking only the mentioned high to medium cloud probability with a 200 m buffer was therefore chosen as a trade–off between data availability and quality.

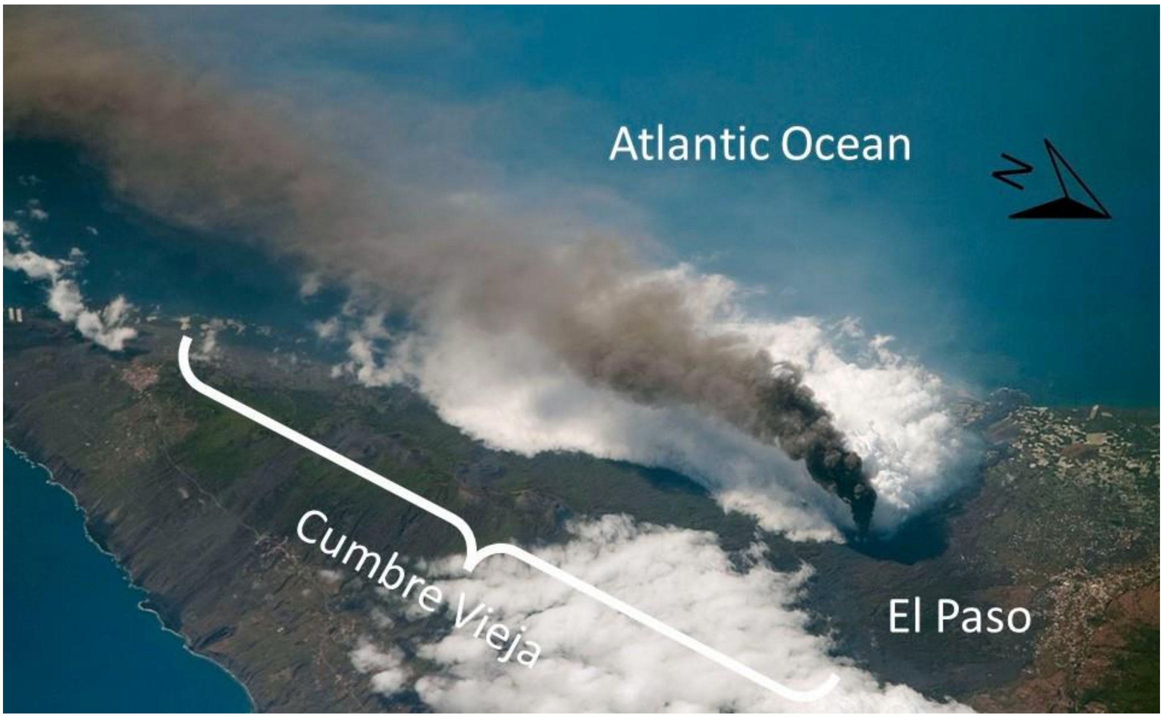


Figure 3. View of the southern part of La Palma from space on 4 October 2021. This picture reflects the characteristic wind direction in the troposphere from NNE. The dark plume of ashes at the higher altitude is clearly distinguished from the cloud formation below, enhanced by volcanic aerosols. The most common cloud formation caused by the prevailing NE tradewinds (lower rim of the picture) usually dissolves when passing over the ridge (Foto NASA).

The normalized difference vegetation index (NDVI) was calculated for all images. Distance from the eruption craters was calculated from the Copernicus EMS data [13] from 9 December. The position of each forest pixel in relation to the eruption was also calculated from this dataset.

The NDVI was calculated for both scenes (30 November 2019 and 14 December 2021) using the following Equation (1):

$$\mathrm{NDVI} = (\mathrm{NIR} - \mathrm{red})(\mathrm{NIR} + \mathrm{red}) = (\mathrm{Band}\ 8 - \mathrm{Band}\ 4)(\mathrm{Band}\ 8 + \mathrm{Band}\ 4) \tag{1}$$

An NDVI difference map (from here denoted "ΔNDVI") was created by subtracting the NDVI before the volcanic eruption from the NDVI afterwards. We used the ΔNDVI as a proxy for vegetation damage. The ΔNDVI was extracted using the packages "rgdal"1.5–23 [57] and "raster" version 3.4–5 [58] in R version 3.6.3 [59].

An expert-based land cover classification provided by the Cabildo Insular de La Palma (island council) was used as a forest mask for the Canary pine forest. Since the official land cover classification contains some forest gaps and areas with very low forest cover, which negatively influence the pixel-based analysis, it was combined with the Copernicus tree cover density product [60]. A threshold of 50% minimum tree cover was selected, based on visual inspection of problematic areas. We used a combination of both products to extract the pine forest from the Sentinel-2 images. These natural forests exhibit mono-dominant stands of *P. canariensis* in the canopy. For this reason, no interference with other tree species needs to be considered. Ash deposits also influence vegetation changes detected with the NDVI. Bare ground of volcanic origin in the study area covered with fresh ash showed lower NDVI values than before. This also influenced the decline in NDVI detected in forest pixels with little canopy cover. The combined forest mask starkly reduced this problem, as it only kept forest pixels with reasonably high canopy cover. Additionally, visual inspection of the true-color images created from the Sentinel-2 scenes and compared to the ΔNDVI showed a strong decline in NDVI in trees with visible chlorosis and no or little decline in NDVI in nearby healthy trees. Therefore, ash deposits on needles had little effect on the calculated ΔNDVI values in this study.

Data on sulfur emissions were acquired from the Sentinel-5P TROPOMI product focused on atmospheric concentrations (Figure 4). Sentinel-5P is contributing to the Copernicus Atmospheric Monitoring Services (CAMS). These services inform us about air quality and pollution, with SO_2 as a main data product (see Table 1). The total amount of SO_2 emitted from the eruption per day was retrieved from the Instituto Geológico y Minero de España (IGME) [33]

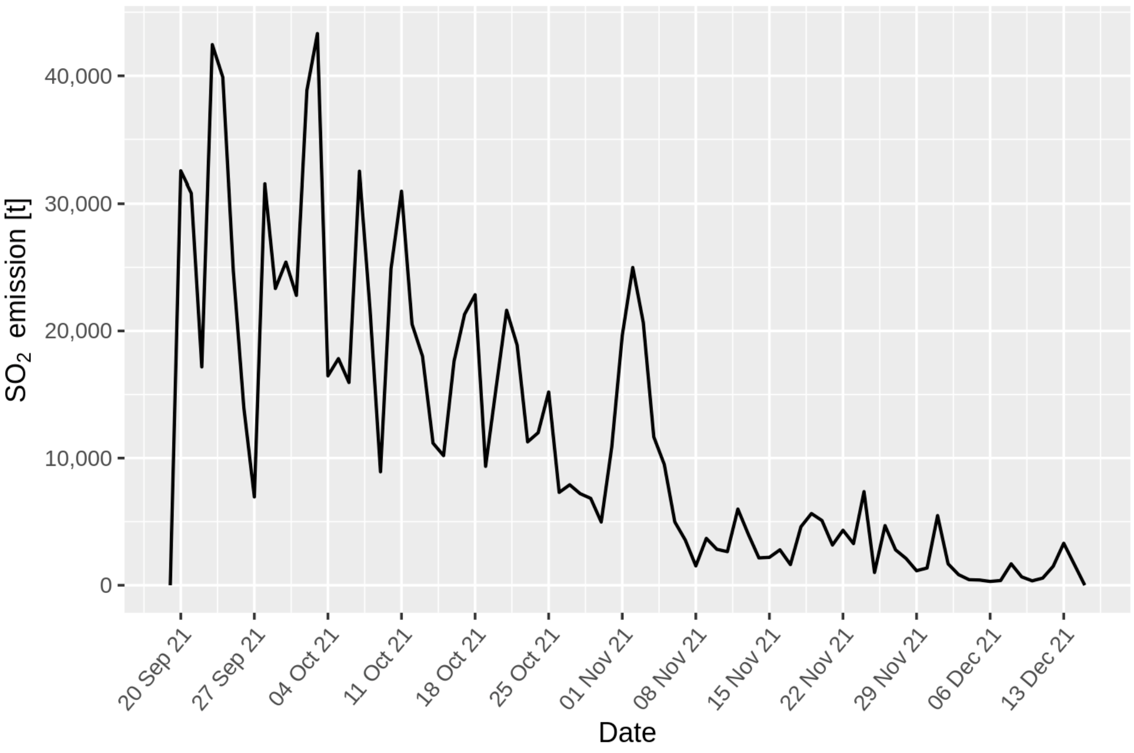


Figure 4. Time series of the daily sulfur emissions during the volcanic eruptions at Cumbre Vieja, La Palma, between 19 September and 14 December 2021. These were concluded from the Sentinel-5P TROPOMI measurements of SO_2 concentrations in the atmosphere. Series based on measurements by Sentinel-5P and NASA Suomi-NPP/OMPS. Data source: "© Geological Survey of Spain (IGME)".

Table 1. Remote sensing products and data sources used in this study.

Product	Data Basis	Source
NDVI	Sentinel-2 (11 November 2019 and 14 December 2021)	Copernicus, preprocessed with "sen2R"
Forest mask	Land cover classification and Copernicus tree cover density	Cabildo Insular de la Palma and Copernicus
Distance and direction from eruption Elevation and topography	Copernicus Emergency Management System (EMS) LiDAR-based 2 m digital elevation model	Copernicus EMS
Atmospheric sulfur	Sentinel-5P/NASA Suomi-NPP/OMPS	Instituto Geológico y Minero de España, CSIC, Instituto Geográfico Nacional

To estimate sulfur deposition in the study area, the weather data during the eruption were acquired from the Cabildo Insular de La Palma weather station at Cumbre Nueva (28°38′49′′ N 17°49′30″ W), situated 5.5 km northeast of the eruption. Due to a technical failure of the radio transmitter at the weather station, only data before 22 November 2021 were available. This station measured wind speed, direction, and other meteorological variables every 10 min. Very few data gaps were present, but one day (30 September 2021) was removed from the dataset due to more than two hours of data being missing. Daily SO_2 emissions were divided by the number of daily wind observations (Figure 5). This combination was plotted using the R package "openair" version 2.8-6 [61]

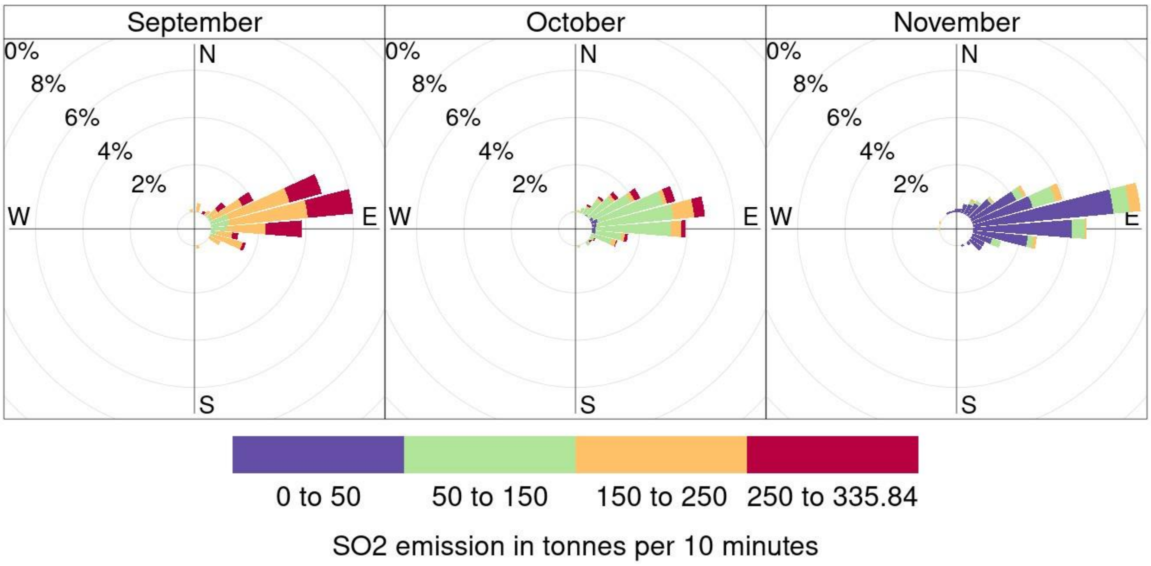


Figure 5. Windroses indicating the frequency of wind directions during the volcanic activity phase on La Palma. The weather station is located 5.5 km northeast of the new volcano on the ridge of Cumbre Nueva (28°38^{t}49^{tt} N 17°49^{t}30^{tt} W). Data extend from 19 September 2021 to only 21 November 2021, due to technical failure. Wind data were recorded every 10 min with occasional data gaps. One day (30 September) was deleted from the dataset due to more than 2 h of missing data. Daily sulfur dioxide emissions were divided by all wind measurements on the same day. The length of each wedge shows the percentage of wind from that direction, color indicates the amount of SO_2 emissions in metric tons per 10 min. Data sources: wind – Cabildo Insular de La Palma (wind), SO_2— "© Geological Survey of Spain (IGME)".

3.2. Data Analysis

Connecting the changes in the NDVI in direct comparison before and after the event allowed us to quantify the spatial patterns of vegetation damage. Here, we link these patterns of NDVI change with the probability of deposition of sulfur compounds, derived respectively from the recorded daily emissions and from the recorded main wind directions during these days.

Sentinel-2 sensors deliver appropriate remote sensing information due to their spatial resolution (up to 10 m) and revisit time of 5 days [62]. However, it was difficult to find cloud-free areas during the volcanic eruption because the emitted ashes, smoke, and gases resulted in dense cloudiness during this period.

ΔNDVI was extracted for all Canary pine forest pixels from the combined forest mask. The distance and direction relative to the eruption were also extracted for all forest pixels. We then analyzed the relationship of ΔNDVI to the distance from the eruption, as well as the importance of the relative position regarding the eruption. The dataset was split into three parts: north (315° to 45°), east (45° to 135°) and south of the eruption (135° to 225°). In the western direction (225° to 315°), due to the lava stream only two very small tree stands remained and were therefore excluded. Additionally, we split the ΔNDVI for the southern half of the island (south of the midpoint of Cumbre Nueva ridge) into two parts: east and west of the complete ridge of Cumbre Vieja and Nueva. We then tested if there was a significant difference between forest patches on the wind- or leeward sides of Cumbre Vieja/Nueva. We used the R package "raster" [58] to combine the acquired remote sensing data for analysis.

As a measure of the area of damaged forest, the overall area of forest pixels in our forest mask was calculated. We also calculated the area of pixels with a 10% or stronger decline in NDVI and also with a 20% or stronger decline, then cropped it to the area of Cumbre Vieja and Nueva ridge to exclude pixels with declining NDVI from different unrelated causes on the northwestern coast. We used this area to calculate the percentage of Canary pine forest damaged by sulfur dioxide emissions.

To analyze the relationship between the distance from the eruption and ΔNDVI, generalized linear models (GLMs) were fit to the data. Several data transformations (linear, quadratic, and log) were tried out. We selected the best transformation based on AIC and general model fit, and therefore selected GLMs with the formula ΔNDVI ~ distance + log(distance). Function "pseudoR2" from the package "DescTools" version 0.99.40 [63] was used to calculate Nagelkerke's pseudo-R^2 value for all GLMs.

4. Results

A clear spatial pattern emerged from Earth observation of NDVI change when comparing the greenness of the pine forest before and just after the volcanic activity. A large proportion of natural Canary pine forest stands on the western slope of Cumbre Vieja showed chlorotic responses to the eruption. True-color images created from Sentinel-2 revealed that the discoloration of the canopy, which can be seen in the field (Figure 6), is also clearly visible in Sentinel-2 images and can be detected for many parts of the Canary pine forest in the surroundings of the eruption.

Figure 6. Chlorotic discoloration of Canary pine forest in the vicinity of the volcanic eruptions. Image taken on 10 November 2021. (Photo: Félix M. Medina).

ΔNDVI revealed a clear spatial pattern of the damage to the forest canopy—most trees on the western slope of Cumbre Vieja exhibited a strong decline in greenness. This decline is visible for at least 7 km south of the eruption crater, while forest patches on the outer slopes of the Caldera de Taburiente and Cumbre Vieja to the north of the eruption craters exhibited a weaker decline in NDVI (Figure 7). The decrease in greenness in the vicinity of the eruption crater showed a clear relation to distance; forest patches closer to the crater had a stronger decline in NDVI compared to those further away (Figure 7). Overall, the NDVI decrease due to visible chlorosis was clearly located mostly in the area around the eruption and fits visual field observations of such damage. Pine forests in other areas of the island exhibit similar NDVI values in 2021 when compared to 2019. The few small spots of visible NDVI decline elsewhere on the island cannot be linked to visible chlorosis and most likely had different sources, e.g., atmospheric effects, declining vegetation health for other reasons or image artifacts. Of the 183 km^2 of forest in our forest mask, 18.8 km^2 (10.3%) showed an NDVI decline of 10% or more, while 13.4 km^2 (7.2%) underwent a decline of 20% or more. The damaged area lies almost completely within the area protected under Natura 2000.

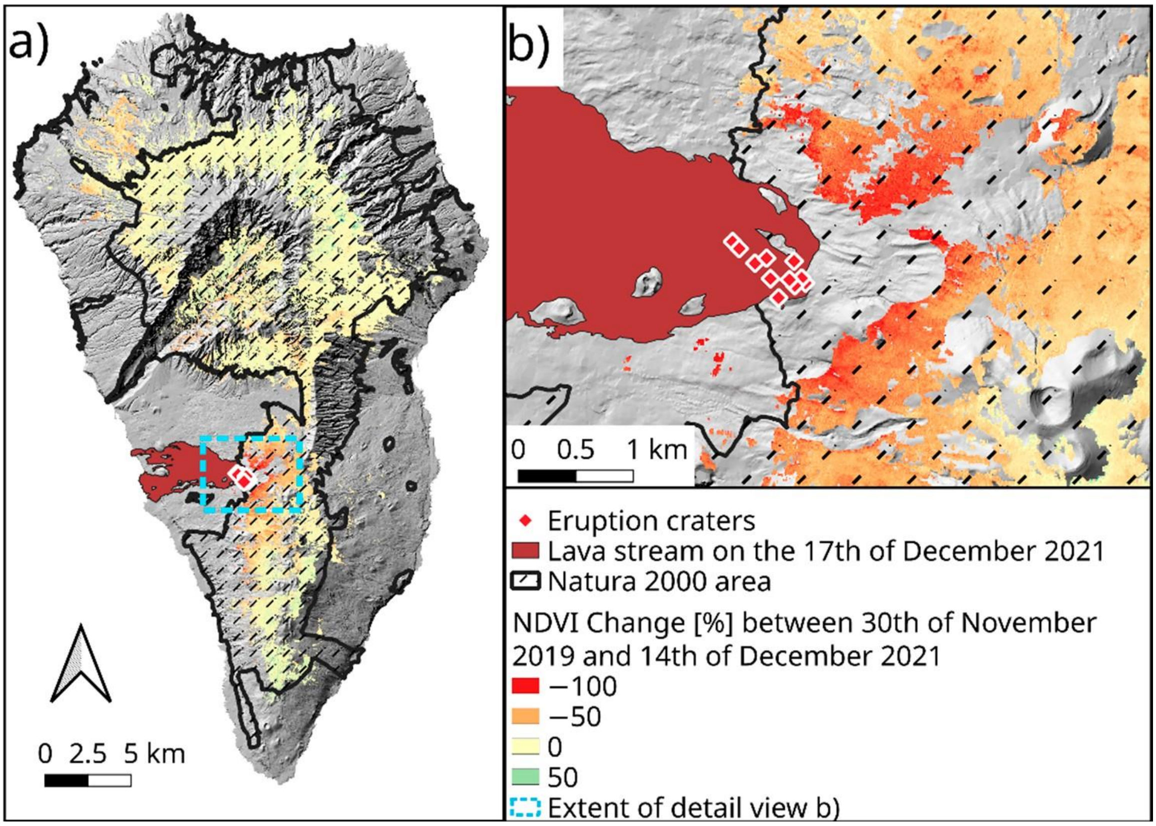


Figure 7. Impact of the 2021 eruption on La Palma's endemic pine forest. Red diamonds indicate eruption sites, and the lava stream is shown in brown–red. The area outlined and shaded in black marks terrestrial Natura 2000 areas. Green, yellow, orange, and red show the NDVI change, in percent, within the pine forest area before (30 November 2019) and after the eruption (14 December 2021). The turquoise frame in the overview map (**a**) marks the extent of the detailed view (**b**). Some minor parts of the forest are not shown in the NDVI product due to cloud cover. Yellow coloration indicates no change, orange and red a decrease in greenness as an effect of the eruption, and green an increase in greenness. Background map: Hillshade generated from a digital elevation model.

Figure 8 shows the relationship between ΔNDVI and the distance from the eruption craters for 100,000 random points within the pine forest. A clear pattern is visible, with the highest decline in NDVI, up to 100%, closest to the crater and smaller declines further away. At roughly 7 km, the majority of forest pixels show only limited or no NDVI change due to the eruption. Nonetheless, there are several groups with a strong (30–50%) decline in NDVI at larger distances, e.g., at 8 and 10 km. A GLM with the formula ΔNDVI ~ distance + log(distance) showed a significant relationship between ΔNDVI and distance, and had a Nagelkerke's pseudo-R^2 of 0.41.

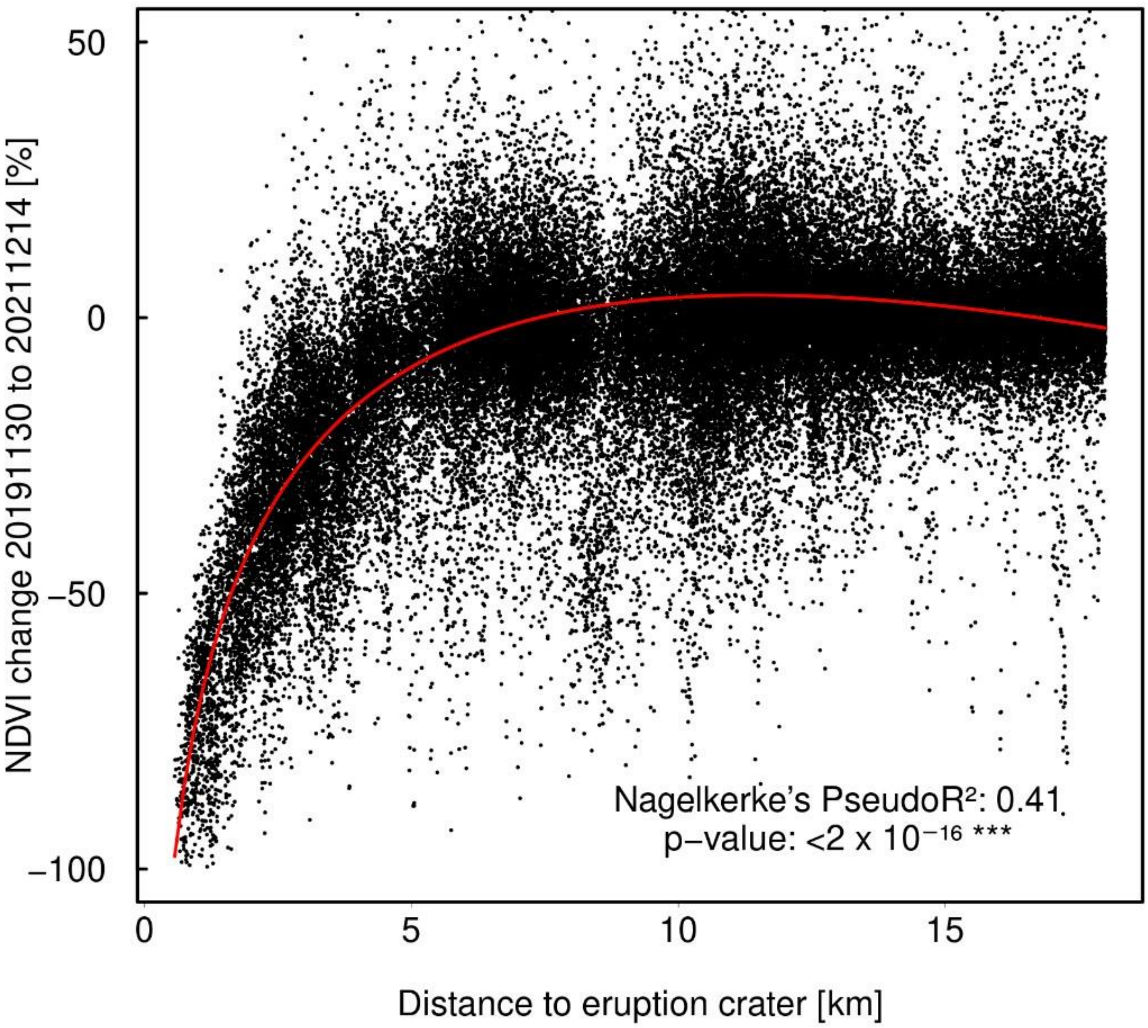
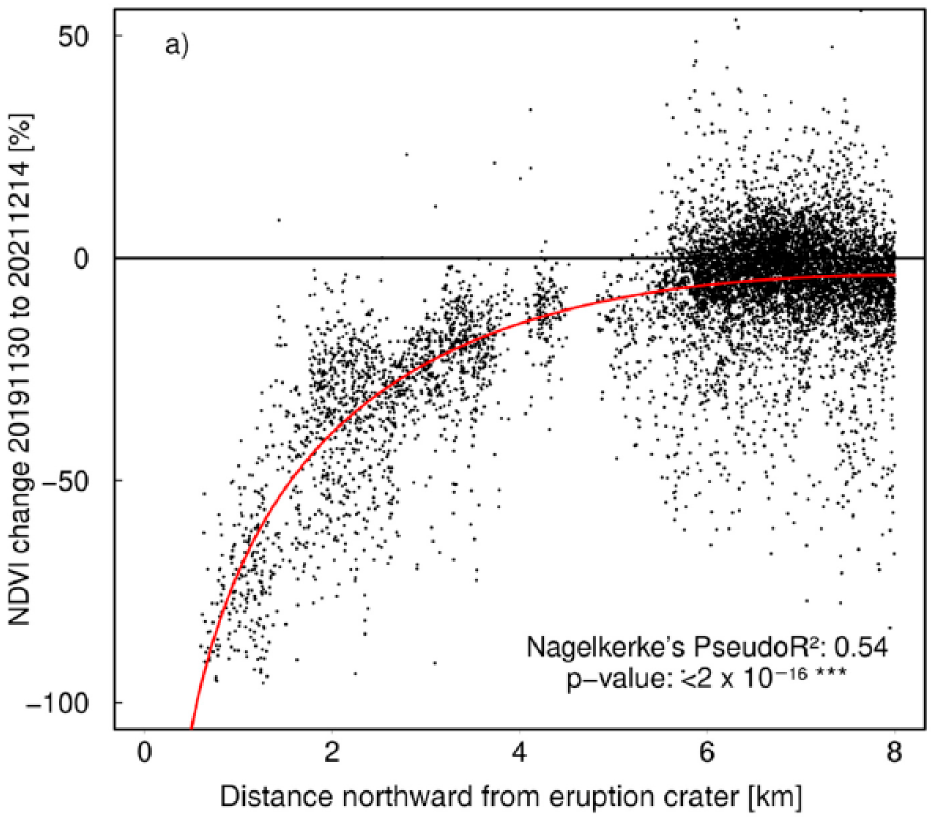


Figure 8. Relative change in the normalized difference vegetation index (NDVI) between 30 November 2019 and 14 December 2021, against the distance to the eruption craters (based on data from Copernicus EMS from 9 December 2021) for 100,000 random data points within the Canary pine forest. The distances shown were limited to the first 18 km, with forests at larger distances (up to 25 km) excluded. The red line represents a highly significant (***) GLM of the formula ΔNDVI ~ distance + log(distance) with a Nagelkerke's pseudo-R^2 value of 0.41.

The three subsets representing forests north, east, and south of the eruption show only slightly different relationships between NDVI decline and distance from the eruption (Figure 9). Forests south of the eruption had more affected forest patches closer to the crater compared to the areas northward, at least for the nearest 5 km. This is expressed by the fitted curve for the southward direction, which runs consistently below the curves for northward and eastward for distances between 2 and 5 km, indicating more severely damaged forest patches for those distances. The eastern dataset shows a steeper increase, with most forest pixels roughly 4 km away from the eruption already exhibiting only little to no decline in NDVI. The corresponding GLMs are all highly significant and have pseudo-R^2 values of 0.54, 0.61, and 0.48, respectively.



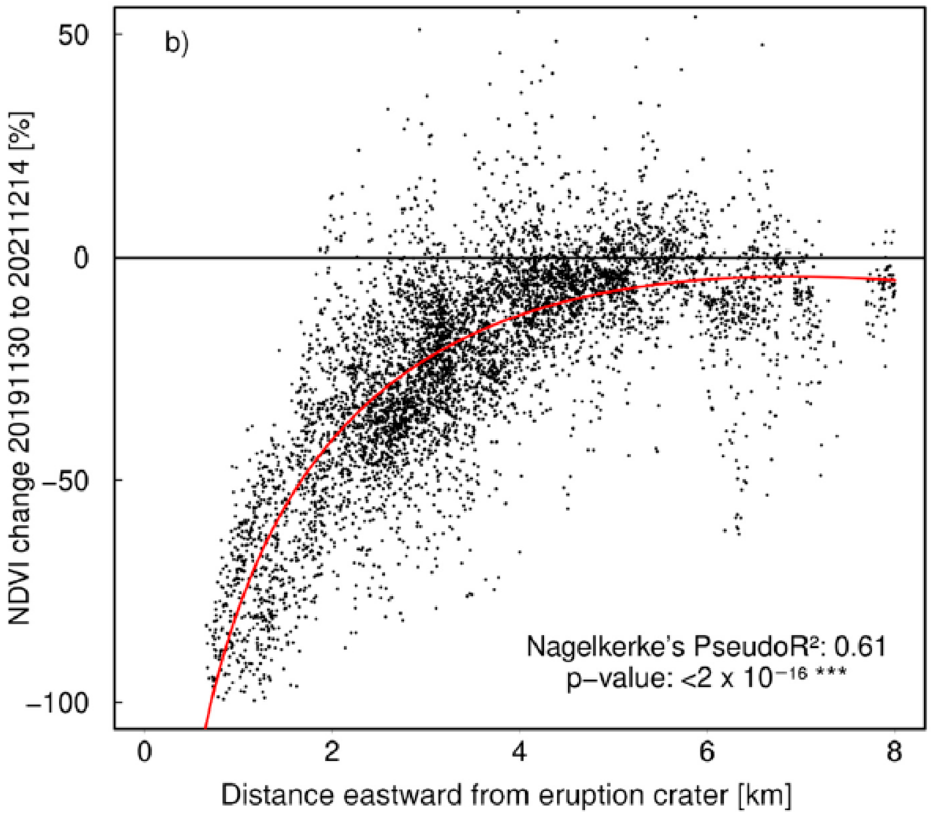


Figure 9. *Cont.*

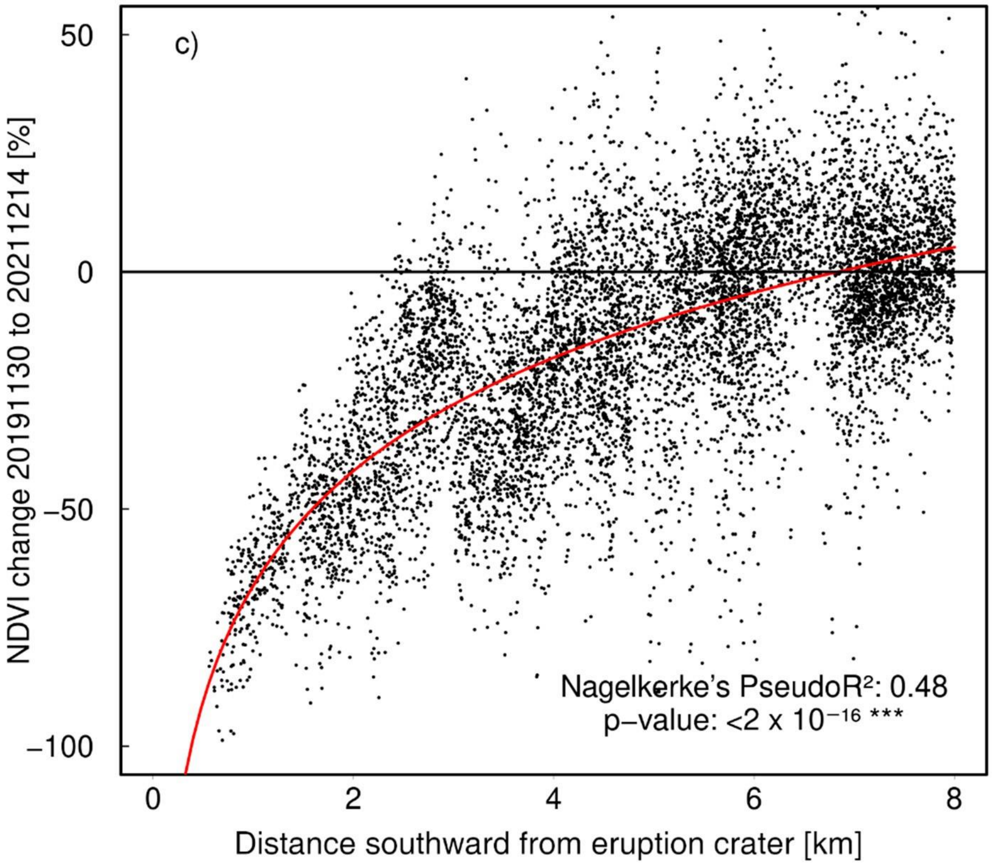


Figure 9. Relative change in the normalized difference vegetation index (NDVI) between 30 November 2019 and 14 December 2021, against the distance to the eruption craters (based on data from Copernicus EMS from 9 December 2021). The 100,000 random data points extracted from both rasters were split into three subsets: (**a**) north of the eruption (225° to 315°), (**b**) east of the eruption (135° to 225°), and (**c**) south of the eruption (45° to 135°). Apart from two very small tree stands situated west of the eruption, most trees in this direction were covered by lava. This direction was, therefore excluded from the analysis. The red lines represent a highly significant (***) GLM of the formula ΔNDVI ~ distance + log(distance) with Nagelkerke's pseudo-R^2 values of 0.54, 0.61, and 0.48, respectively.

5. Discussion

The strong impact of the volcanic eruption on the Canary pine forest is difficult to explain by heat, even if fluid lava was hotter than 1000 °C. Heat impact would only be effective in close proximity to the lava. Other impacts related to the volcanic activity, such as emission of CO_2 and volcanic ashes, are also unlikely to result in chlorotic discoloration of pine needles. Ash initially covered a large amount of pine trees, but was removed by wind and rain. The evergreen pine forest did not show substantial seasonal variation in spectral traits of the canopy. Seasonal patterns as a response to precipitation, however, can only be expected for the herbaceous vegetation in the understory. As a consequence, canopy density needs consideration to avoid a strong influence from the phenology of field layer vegetation. This was performed in this study, based on a digital tree cover product, we considered only forest surfaces where tree cover was >50%.

In addition to the distance related decay in plant damage, we also found a weak anisotropic distribution with stronger impact southward from the volcano. Indeed, the western lowlands downslope are mainly covered by land use and settlements. The eastern slopes were protected from the eruption by the Cumbre Vieja ridge and, more so, the then prevailing wind direction. The major wind directions during the eruptive phase were ENE and E, which explains this asymmetric pattern of damage. However, overall, the anisotropic relationship was weak, indicating that most of the SO_2 emission reaching the pine forest was omnidirectional. This is supported by the wind direction data. Especially during the early days of the eruption, the wind blew nearly exclusively from the east and northeast, distributing SO_2 towards the west. On many days, wind speeds were also low, causing volcanic gases to rise into higher atmospheric layers before being spread. The 2021 La Palma volcanic eruption was intensely monitored, both in the field and by Earth observation [64]. Many scientists and institutions, such as the Spanish National Geographic Institute (IGN), Canary Islands Volcanology Institute (Involcan), Spanish National Research Council (CSIC), Univerisity of la Laguna (ULL), University of Las Palmas de Gran Canaria (LPGC), Cabildo Insular de La Palma, and the Canary Islands Government were involved, among others. This intense survey is providing invaluable data resources that will improve our understanding of volcanic impacts. In addition, worldwide attention and the European Copernicus Earth Observation program have yielded Big Data and geospatial information. Here, we focus only on a small section of this treasure, to point out the direct ecosystem responses during and immediately after the eruption. We are convinced that many other studies will follow.

Through Earth observations, negative impacts on the endemic Canary pine forest ecosystems—among which the volcanic cones emerged—can be precisely documented, as in in this study. Evidence suggests that gaseous emissions are the main driver of these responses. Such natural pollution events took place frequently in the Earth's history, but cannot easily be traced back due to their elusive and ephemeral properties [65,66]. Nevertheless, as shown in this study, the effects of such cases of natural pollution can be substantial. In the case of La Palma, 10.3% of the island's pine forests and 5.2% of its protected areas have been affected, and they host many unique endemic species. Currently, it is too early to say whether the small populations of endemic plant species located in the southern half of the island have been severely affected. However, according to field observations, they have not been driven to extinction yet. Only a wild chickpea *Cicer canariense* A. Santos & G.P. Lewis and a new species currently named *Parolinia aridanae*, description pending [67], are potentially threatened plants, but to date their conservation is not compromised [68].

The island of La Palma can be seen as a natural laboratory to study ecological, geomorphological, and biogeochemical processes [69,70]. The high degree of naturalness of ecosystems reduces confounding anthropogenic influences. The volcanic eruption at Hoya de Tajogaite in 2021 was the largest such event within historical times on La Palma. Records of previous eruptions date back to 1450, which are still visible as uniquely distinct lava flows. However, the vast lapilli fields on Cumbre Vieja ridge cannot be attributed directly to individual volcanic cones or events. Furthermore, likely chemical impacts in the past are not reflected, protocolled, or preserved. Volcanic gases are transient, but have a strong impact on vegetation near eruptions, which is surprisingly little studied (e.g., [71–73]). In 2021, the amount of sulfuric compounds released was precisely protocolled on a diurnal basis. In combination with recorded wind directions, it allows us to assess the spatial influence of sulfuric gases on the ground. No other hampering impacts, such as fire or drought, occurred in this short period. Thus, it is most likely that the NDVI change was caused by the enormous amounts of sulfuric emissions.

In contrast to the widespread literature dealing with fire impact on Canary pine and on the dynamics of its forest ecosystems (e.g., [37,43,44,48,74], research was lacking until now on the impact of volcanic gases on these trees and forests. However, such events occurred frequently during the existence of the archipelago. The impact of pollutants, including sulfuric compounds, on this pine were hitherto only studied in connection with anthropogenic environmental pollution related to car traffic [75]. Exposure to such types of pollution, however, is many orders of magnitude lower than the toxic compounds released from this recent eruption. The total amount of SO_2 emissions during the active phase of the volcano was enormous, even if the real sulfur emissions cannot be measured precisely while released during that phase. Estimates range up to 1 Tg (1,000,000 tons) of SO_2 [33], which makes this event important at a global level.

Atmospheric measurements from space deliver good proxies and estimates for the order of magnitude. Local measurements of air pollution in settlements that aim at health care are less representative of landscape-scale pollution impacts. In this study, we decided to use data from satellite sensors due to their spatial cover, methodological standardization, and daily availability. Data from different sensors deviate due to technological factors (e.g., Sentinel-5P TROPOMI vs. Nasa Suomi-NPP/OMPS). In this study, this is less relevant as we are interested in the spatial patterns of the impact on the ground. A substantial proportion of the emitted sulfur compounds are projected into the high strata of the atmosphere and transported over long distances, without contact with land surfaces and ecosystems. Nevertheless, satellite sensors can inform on the quantitative development of emissions for every single day. This helps to understand the role of prevalent wind directions and to identify processes leading to the anisotropic distribution of pine damage on La Palma, in addition to the mere distance from the source of emission. On a global scale, sensors from the Copernicus program can be combined to monitor the distribution of emitted SO_2 and to investigate forest responses to such events.

The general importance of volcanic eruptions and gas input in atmospheric chemistry has been highlighted [76,77]. Particularly, emissions of CO_2 and SO_2 are seen as substantial contributions to changes in atmospheric chemistry. However, there is little knowledge about the effects of such gaseous emissions on terrestrial ecosystems. The chlorotic and necrotic responses of pine needles are documented as related to atmospheric sulfur exposure [78], but the ecological literature on atmospheric sulfur impacts is mostly focused on industrial pollution and acid rain (e.g., [79]). As a consequence, these studies are strongly biased towards northern-hemisphere conifer forests. However, it is crucial to better understand the role of such temporarily limited events in ecosystem and biodiversity dynamics [66].

Andres and Kasgnoc [80] compiled the first global inventory of subaerial volcanic sulfur emissions, based on SO_2 measurements en situ. Using data from the second half of the 20th century, they estimated an annual average of 13 Tg SO_2 emissions from volcanoes. This worldwide quantity illustrates the importance of the 2021 eruption on La Palma, with approximately 1 Tg SO_2 emissions. Recently, several groups studied volcanic SO_2 emissions with the support of remote sensing [81–83] and modeling [84]. However, there are few studies on the impact of volcanic gases on vegetation [31]. The recent volcanic eruption on La Palma provided a chance to study this fundamental process that happened so frequently in the Earth’s history. Highly precise monitoring of the volcano during its active phase, together with Earth observation data, quantification of sulfur emissions from space, and detection of vegetation responses has offered an unprecedented opportunity. The pattern identified will also serve as a reference for future changes in the drivers of ecosystem changes and responses in the biodiversity [85,86].

6. Conclusion

The eruption on the west slope of Cumbre Vieja (La Palma, Canary Islands, Spain) gained global attention. This event developed into the strongest and longest-lasting eruption in the island's historical records. The emission of ashes and gases had a far-reaching impact, besides the large lava field that now covers former settlements, agricultural fields, and semi-natural vegetation, along with two new volcanic deltas (*fajanas)* on the coast. Here, we focused on the effects of gaseous emissions, in particular SO_2 and its derivate compounds such as sulfuric acid, on the endemic pine forest of the island. This forest is largely protected through Natura 2000 and is of decisive importance for ecosystem services, such as the provision of freshwater and carbon sequestration.

We successfully used remote sensing-based analyses to find a clear spatial pattern that can be explained by distance decay towards the source of eruption. Chlorotic damage to the pine forest canopy was clearly visible in the Sentinel-2 earth observation data. Due to the lack of large forests to leeward of the eruption, we were not able to prove nor disprove the importance of wind direction and only found a weak anisotropic pattern. Stands of *P. canariensis* are known to exhibit high resilience towards disturbances, providing a unique study ground for testing an emerging theory on pulse dynamics in ecosystems [66]. This tree species resprouts after fire impact and total defoliation. For this reason, we expect this forest ecosystem to recover in the following years. This study also serves as comparison for future monitoring of ecosystem recovery. The specific conditions during the active phase released a large amount of acid aerosols that caused cloud formation in addition to the frequent plume or fan of ashes and smoke from the volcano. Nevertheless, this location on the less humid leeward side of the island will provide many cloud-free days in the future to monitor how the affected pine forests recover.

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6.3 Manuscript 3

Discoloured *Pinus canariensis* stands close to the eruption crater

Combining in-situ monitoring and remote sensing to detect spatial patterns of volcanic sulphur impact on pine needles

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Authors: Frank Weiser[1*], Anna Walentowitz[1], Esther Baumann [1,2], Christopher Shatto[1], María Guerrero-Campos [3], Anke Jentsch[4], Manuel Nogales[5], Félix Manuel Medina[6], Ole R. Vetaas[7], Carl Beierkuhnlein[1, 8, 9]

Affiliations:

[1] Biogeography, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany,

[2] Biomasseinstitut, BIT, University of Applied Sciences Weihenstephan-Triesdorf, Markgrafenstr. 16, 91746 Weidenbach, Germany

[3] Área de Medio Ambiente, Gestión y Planeamiento Territorial y Ambiental (Gesplan S. A.), Tenerife, Canary Islands, Spain

[4] Disturbance Ecology and Vegetation Dynamics, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany

[5] Island Ecology and Evolution Research Group, Institute of Natural Products and Agrobiology, Spanish National Research Council, La Laguna, Tenerife, Canary Islands, Spain,

[6] Consejería de Medio Ambiente, Cabildo Insular de La Palma, Canary Islands, Spain

[7] Department of Geography, University of Bergen, 5020 Bergen, Norway

[8] Bayreuth Center for Ecology and Environmental Research BayCEER, D-95440 Bayreuth, Germany

[9] Geographical Institute Bayreuth GIB, D-95440 Bayreuth, Germany

***corresponding author:** frank.weiser@uni-bayreuth.de

Abstract

Volcanic eruptions have a strong environmental impact on surrounding forests. Trees are affected by mechanical damage, tephra deposition and volcanic gases. Oceanic islands are shaped by relatively frequent volcanic eruptions and thus offer the opportunity to study their effects on biodiversity. We investigate the impact of volcanic gas emissions and tephra deposition during the 2021 Tajogaite eruption on the Canary Pine forests of the island of La Palma, Spain, , characterized by monospecific stands of the endemic pine species *Pinus canariensis* C. Sm. Ex D.C.. Large quantities of volcanic sulphur dioxide caused chlorotic damage up to approximately 7 km around the crater, followed by widespread resprouting of *Pinus canariensis* C. Sm. Ex D.C.

To detect the spatial pattern of impacts, we sampled *P. canariensis* needles from all over the island of La Palma and analyzed their sulphur (S), nitrogen (N) and carbon (C) content. We found a strong increase of S needle content close to the crater, while C and N both decreased. S levels were strongly related to distance to the crater, C and N were mostly influenced by S content, and thus inversely related to distance to the crater. Trees affected by volcanic gases allocate resources to resprouting (primary needles), leading to lower levels of C and N in secondary needles.

In addition, we investigated how canopy damage patterns detected in Sentinel-2 remote sensing imagery in several timesteps after the eruption correlates to the in-situ needle contents. However, we could not find a clear correlation between in-situ needle values and spectral responses in remote sensing. While satellite images were well suited to analyse large scale patterns of canopy damage following the eruption, needle levels varied strongly on a local, tree-based level, which is not reflected in remote sensing imagery.

Key words: *Pinus canariensis*, volcanism, sulphur, disturbance, pulse dynamics, earth observation, remote sensing, Sentinel-2, leaf chemistry

1. Introduction

Volcanism is a natural and prominent component of the pulsed disturbance regime (Jentsch & White, 2019) of oceanic islands. While volcanic eruptions create, enlarge, and topographically change islands, they can initiate or even reshape or destroy local ecosystems and their biotic assemblages (Whittaker & Fernandez Palacios, 2007). The physical and geochemical processes and their ecological consequences are manifold and differ in intensity and scale, ranging from large scale catastrophic events yielding abrupt change in ecosystems (Turner et al., 2020) to local impacts with re-assembly of fluxes and biota. The Canary Islands are well suited to study the effects of volcanic eruptions. The Canary Islands Seamount Province formed at the edge of the African plate since the spreading of the Atlantic Ocean at the end of the Jurassic (van den Bogaard, 2013). The current emerged islands range in age between 1.12 and 20.6 Ma (Carracedo, 1999).

Volcanic activity does not only shape the islands but also strongly impacts their biota. Gran Canaria is assumed to have been effectively sterilised 5.6 Ma to 3 Ma ago (Pérez-Torrado et al., 1995) causing a total reset of evolution and biodiversity (Marrero & Francisco-Ortega, 2001; Emerson, 2003). During the last 500 years, at least 14 volcanic eruptions have occurred on the Canary Islands, seven of them on La Palma (Longpré & Felpeto, 2021; Longpré, 2021). While volcanic activity in the Canary Islands has been intensely studied (e.g. Carracedo et al., 1998), less research has been done on their effects on ecosystems and vegetation (Irl et al., 2019).

Ecological impact studies on vegetation and ecosystems remain cursory and can hardly be generalised due to substantial differences in volcanic activity. There is evidence of physical damage through volcanic bombs and pyroclastic flows (Rodríguez Martín et al., 2013), deposition of tephra (Mack, 1981; Zobel & Antos, 1997; Kent et al., 2001) and chemical damage through volcanic gases (Clarkson & Clarkson, 1994).

The eruption of the Tajogaite volcano on the island of La Palma, Canary Islands lasted from 19th of September 2021 until 13th of December 2021. This is the longest reported eruption on this island in historical records (Longpré & Felpeto, 2021). The eruption displaced 6400 residents (Longpré, 2021) and its lava stream covered an area of 1241 ha and destroyed 2988 buildings and 92.1 km of roads (Copernicus Emergency Management Service, 2021). The eruption emitted toxic gases, e.g., roughly 1 Tg SO_2 and thus, strongly affected the flora and fauna within a radius of 2.5 km (Nogales et al., 2022) and causing chlorotic damage to the surrounding forests up to 7 km (Weiser et al., 2022).

The Canary pine forest was particularly affected due to the location of the new volcano along the slope of Cumbre Vieja. This ecosystem has evolved under the legacy of volcanic eruptions and is well adapted to these (López de Heredia et al., 2014) as well as other disturbances, such as fire (Climent et al., 2004). *Pinus canariensis* can withstand heavy metal pollution associated with volcanic eruptions (Rodríguez Martín et al., 2013). This tree species can resprout from all woody organs (Pausas & Keeley, 2017), can colonize fresh volcanic tephra deposits (López et al., 2013) and is physiologically adapted to different climatic conditions (Miranda et al., 2021). Nevertheless, the pine forest canopy showed chlorotic damage as an effect of volcanic activity (Weiser et al., 2022) (Figure 1). Besides toxic gas impacts, needles were physically covered by ash and individual specimens had to withstand several meters of tephra deposits. These tephra deposits further leach sulphur (S) during weathering, which is controlled by fragment sizes, compaction, porosity, and moisture (Hoffer & Hoffer, 1986; Zobel & Antos, 1991; Delmelle et al., 2005). Additionally, the contained volcanogenic S and integrated organic litter are important components of soil formation on tephra deposits (Cronin et al., 1998; Ayris & Delmelle, 2012).

Figure 1: Individuals of *Pinus canariensis* sticking out of approximately 3 m of Tephra close to the volcanic crater of Tajogaite. Both needles with severe chlorotic damage and resprouts are visible. (Photograph: Anke Jentsch).

Pinus canariensis often occurs in sites with limited resource availability. After suffering damage or during dry periods, it limits or stops its radial growth to conserve carbon (C) (Miranda, 2017; Lopez et al., 2021) and translocates C for resprouting (Miranda et al., 2020). Therefore, we expect high sulphur (S) levels in needles are linked with low carbon (C) needle content (1). In addition, soils in Canary Pine forest contain low amounts of nitrogen (N) (Durán et al., 2010a), which is further reduced after fire due to erosion and a loss of soil microorganisms. *P. canariensis* generally exhibits comparatively low needle levels of N, which further decrease after fire (Durán et al., 2010b). Following the volcanic eruption, we expect a similar decrease in N due to the negative effects of sulphur deposition on soil microbiota and N translocation in *P. canariensis* during resprouting. Thus, we expect high sulphur levels to be correlated to low needle N levels (2)

We further hypothesize (3) that sulphur levels in needles mirror the detected canopy damage observed as a change in the Normalized Difference Vegetation Index (NDVI).

2. Methods

2.1. Needle selection

Needle samples were collected approximately four months after the end of the eruptive phase between the 31st of March 2022 and the 20th of April 2022. Samples were obtained all over the island of La Palma by randomly collecting needles 1 to 2 m above the ground. To ensure comparability, only mature tree needles from adult trees were sampled. Primary needles, that can also sprout from adult trees under stress, were not included (heteroblasty; Climent et al., 2006, Pardos et al., 2009). Wherever possible, fully elongated secondary needles were sampled. Since *P. canariensis* grows throughout the entire year, this was not always possible (Tausz et al., 2004), especially given the short time window for resprouting following the volcanic eruption. To account for this possible bias in statistical analysis, the length of 10 needles was measured for each sample.

Out of 351 samples, all samples located in areas with less than 50% canopy cover in the Copernicus tree cover product (Copernicus Land Monitoring Service, 2018) were removed to ensure samples can later be jointly analysed with remote sensing data. From the remaining samples, 100 were spatially filtered and selected for S, C and N content analysis. Both within and outside of a 7 km buffer around the crater, a spatial thinning algorithm was applied to the sampling points separately (*spThin* package, Aiello-Lammerns et al., 2015 in R version 4.2.2, R Core Team, 2021) to achieve an appropriate sample size (80 within and 20 beyond 7 km distance). The 7 km buffer was selected based on the distance up to which canopy damage in the Canary Pine forest was detected in remote sensing images in Weiser et al. (2022). The thinning algorithm took the environmental variables elevation, distance to the craters, easterness and northerness (expressed as x and y coordinates) into account to select samples covering a broad environmental gradient.

All selected samples were dried, ground and then analysed in the laboratory for their S, C and N content. Before analysing the full sample, needles of a smaller subset were split, and one half of each sample was washed before analysis. Since washing made no significant difference, the rest of the samples were not washed. For S, 100 mg per sample was ground, mixed with 1ml HNO_3 (65%) and then heated to 170°C for 7 hours. Distilled water was added to the sample, and then S content was measured using an Agilent 5800 ICP-OES spectrometer. Both C and N were measured in a ThermoQuest / Flash-EA 1112 automatic Elemental analyzer.

2.2. Tephra Interpolation

To accurately assess the thickness of the tephra deposited on La Palma, we combined measurements of tephra layer thickness in the field with openly accessible remote sensing data.

This mixed approach was chosen due to the depth of the tephra close to the craters, where time and safety constraints made accurate measurements in the field impossible.

In the field, 415 measurements of tephra thickness were taken all over the island from 30th of March to 20th of April 2022. Measurements were only taken where the tephra layer had not been disturbed yet. Near the location of the 1949 eruption, we differentiated between new ash and tephra deposits of the Tajogaite, and old, oxidized tephra still present in the forest soils. Tephra thickness was measured by manually digging holes to a maximum of 150 cm. Therefore, near the crater particular emphasis was put on getting sufficient tephra depths measurements close to 150 cm to improve the tephra interpolation result.

To appropriately represent the thick tephra layer closer to the crater, two data products were evaluated for their accuracy. The first product used was elevation change data from Copernicus Emergency Management System (EMS) EMSN119 (Copernicus Emergency Management Service, 2022). The data product uses a Spanish Lidar-based Digital Terrain Model (DTM) from 2015 (Centro Nacional de Información Geográfica, 2022) combined with optical Pléiades Tri-Stereo data recorded on the 3rd of March 2022 to calculate a surface change layer for both the lava stream and crater surroundings. The Root Mean Square Error (RMSE) given for elevation calculations of the Pléiades data used is 0.79 m, which is not accurate enough for shallow tephra layers but sufficient for the massive tephra deposits around the craters. The second product evaluated is a Digital Surface Model (DSM) derived from over 12,000 drone photographs coupled with Structure-from-Motion photogrammetry (Civico et al., 2022) with a calculated RMSE of 0.26 m. This dataset was also combined with the Lidar-based DTM.

Both products show nearly identical surface changes over both the crater and the lava stream but differ up to several meters over the ash covered surroundings of the crater. The surface change values of the drone derived model are in much better agreement with our field measurements and observations. We suspect that the uniform surface and colour of tephra covered ground decreases the accuracy of Pléiades Tri-Stereo data in the areas around the craters and lava stream.

Overall, tephra depth was extracted at 66 points from the Civico et al. (2022) product and combined with our field measurements of tephra depth. Extraction points were handpicked because due to the combination of a DSM with a DTM, which measure overall surface and terrain surface respectively, trees are present as a surface change in the resulting difference product. Additionally, surface change results from both ash accumulation and surface deformation of the ground. To minimize inaccuracies, data was only extracted at points where a surface change greater than 3 m was calculated, where no tree cover was present, and where it could be reasonably assumed that the surface change was caused by the tephra layer, not by the cone of the crater.

A deterministic, spatial interpolation of the tephra layer data was performed using Inverse Distance Weighting (IDW) (Figure 2). The interpolation calculation at 2 x 2 m resolution and subsequent surface volume estimation were made using the Geostatistical Analyst and 3D Analyst toolboxes in ArcGIS Pro v.3.0.0 (Esri, 2022). Using IDW, we are able to predict tephra depth at unknown points based on the average distance between sample points. As an exact deterministic method, IDW produces values within the range of measured values (Watson & Philip, 1985). Although geostatistical methods such as original kriging are typically favoured for spatial interpolations (Oliver & Webster, 2014), IDW yielded a better RMSE value for our data (0.455 cm). Furthermore, the total ash layer surface volume was calculated by summing the interpolated surface values above the reference plane across the terrestrial surface of La Palma.

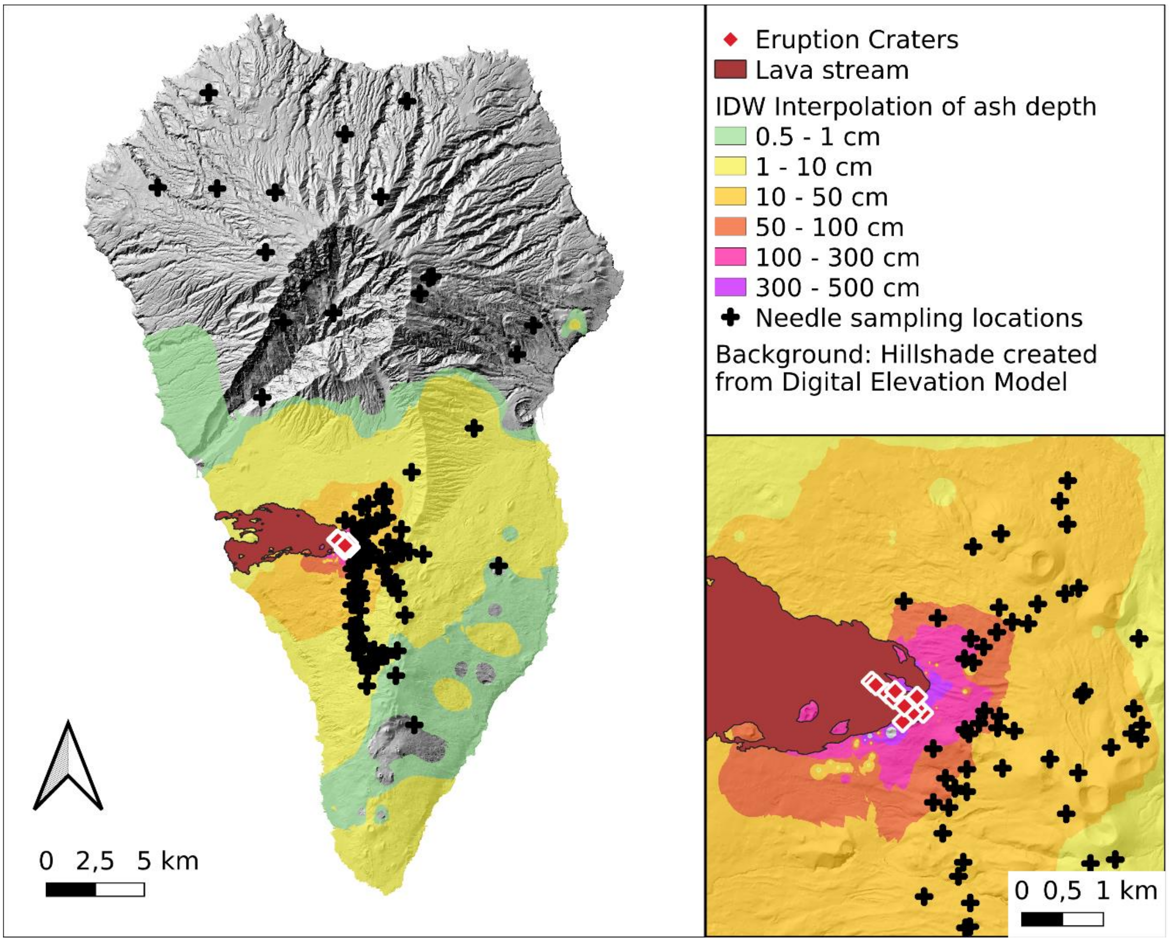

Figure 2: Tephra depth interpolated for the whole island of La Palma. Data basis were 415 field measurements of tephra depth and 66 datapoints around the crater extracted from the difference between a drone-based digital surface model (Civico et al., 2022) and a Lidar based digital elevation model (Centro Nacional de Información Geográfica, 2022). Black crosses mark the 100 needle sampling locations, red diamonds the eruption craters of the 2021 Tajogaite eruption and the dark red shape the lava stream.

To date, few interpolations have been done on the spatial distribution of volcanic ash and tephra deposits following an eruption (Milazzo et al., 2013). With the exceptions of Milazzo et al. (2013) demonstrating the vulnerability of industrial facilities to volcanic ash fallouts and Bellotti et al. (2010) using IDW in their grain size analysis of ash deposits, few studies solely interpolate tephra layer deposition following an eruption. For example, several studies interpolate aerosols disbursed into the atmosphere via volcanic plumes (Gad et al., 2018), tephra beds and soil layers (Shane & Hoverd, 2002; Nakagawa et al., 2011; Nomiyama & Murakami, 2020), and the spatial distribution of metal contaminants (Ma et al., 2019).

On La Palma, Bonadonna et al. (2022) recently investigated the total volume of tephra deposited on La Palma following the eruption in question. Through the stratigraphic analysis of the tephra deposit across the island, they created isopach maps from which they deployed the TephraFits tool (Biass et al., 2019) to estimate the total tephra deposit.

2.3. Remote Sensing analysis

To investigate, whether measured needle parameters correspond to canopy discolouration visible in remote sensing images, nine Sentinel-2 Level 2 images were downloaded and processed using *sen2r,* version 1.5.4 (Ranghetti et al., 2022, Table 1). Images from Orbit 023 and Tile Number 28RBS were selected, taking cloud cover into account.

Table 1: Processed Sentinel-2 images and their purpose for the analysis

Date	Purpose
2019-11-30	Cloud free image before the eruption (only cloud free images not corresponding to the time of year of the end of the eruption were available in 2020)
2021-12-14	Image from the day the eruption ended (some datapoints covered by smoke/clouds above the crater)
2022-01-03	Cloud free image shortly after the end of the eruption
2022-04-18	Cloud free image at the time of sampling, 5 months after the eruption
2022-06-07	Cloud free image 7 months after the end of the eruption
2022-07-27	Cloud free image 8 months after the end of the eruption
2022-10-02	Cloud free image 10 months after the end of the eruption
2022-12-24	Cloud free image one year after the end of the eruption

For all images, cloudy pixels (high and medium probability) were masked out and the Normalized Difference Vegetation Index (NDVI) was calculated, which serves as a proxy for canopy health. All raster calculations after pre-processing were done using the package *terra*, version 1.7.3 (Hijmans, 2023). To minimise the effects of soil in pixels not completely covered by a tree crown, only needle samples from pixels with at least 50% canopy cover in the Copernicus tree cover product were considered. Additionally, the relative change in percentage between image pairs was considered instead of absolute values.

2.4. Auxiliary environmental variables

To investigate influences on S, C and N levels of *P. canariensis* after the eruption, several environmental variables were considered (Table 2). In addition to longitude and latitude, elevation was extracted from a Lidar based digital elevation model (DEM) made available by the Spanish state (Centro Nacional de Información Geográfica, 2022). From this DEM, slope and aspect (transformed to easterness and northerness using the sine and cosine functions) were calculated. Additionally, the topographic position index (TPI) (Gallant & Wilson, 2000) was calculated based on the DEM using the package *spatialEco* version 2.0-0 (Evans & Ram, 2015). For every pixel, the TPI indicates whether the pixel is situated above or below the mean elevation of neighbouring pixels. Depending on how big the considered neighbourhood is, the TPI is a good measure for either local variations in elevation or reveals larger topographic patterns (De Reu et al., 2013; Salinas-Melgoza et al., 2018). Two TPIs names TPI_{15} and TPI_{50} were calculated, considering a 15 m and 50 m radius around each pixel. A large part of the forest affected by volcanic emissions was also affected by the 2016 wildfire (Weiser et al., 2021). To account for the potential decreased vitality of the pre-disturbed trees, the Copernicus EMS grading product was used, which grades affected forest patches in categories of "moderately damaged" or "highly damaged" (Copernicus Emergency Management Service, 2016).

Table 2: Environmental variables used in this study and their source. S = Sulphur, C = Carbon, N = Nitrogen, NDVI = Normalized Difference Vegetation Index, DSM = Digital Surface Model, DEM= Digital Elevation Model, Copernicus EMS = Copernicus Emergency Management Service, TPI = Topographic Position Index

Variable	Data Basis	Source
S/C/N content	Own needle samples	
Tephra depth	Interpolation of field data and DSM derived from drone data	DSM: Civico et al., 2022
NDVI Differences	Sentinel-2 images (see Table 1)	Copernicus, preprocessed with package "sen2R"
- Elevation - Easterness and Northerness of aspect - Slope - TPI	Calculated from 2m resolution DEM	Centro Nacional de Información Geográfica, 2022
Distance to volcano	Calculated from Copernicus EMS	Copernicus EMS EMSR546
Fire severity	Copernicus EMS	Copernicus EMS EMSR173

2.5. Statistical analysis

All statistical analyses were conducted in R (R Core team, 2021). To investigate the relationship between S, C, N and the environmental variables predicting their levels, generalized additive models (GAM) were fitted (Wood, 2006, 2011). To test hypotheses (1) and (2), GAMs of C against S and N against S were fitted. In contrast to simpler models, such as generalized linear models (GLMs), GAMs allow the fitting of a smoothing term to variables to fit non-linear relationships. All GAMs were fitted using package *mgcv* (Wood & Wood, 2015) and used restricted maximum likelihood (REML) to fit the smoothing parameter. For all models, the deviance is reported instead of the adjusted R squared as a more general measurement of goodness of fit (Wood & Wood, 2015).

To check the influence of other environmental variables, GAMs were built for S, C and N each with the variables from Table 2. Fire severity of the 2016 fire event was included as a categorical parameter with three levels: High, moderate and none. Variables were checked for their correlation and again after fitting a GAM containing all environmental variables based on their concurvity, which is a GAM inherent form of co-linearity. Based on concurvity, elevation, both TPIs and the tephra depth were removed. Northerness was removed due to concurvity with easterness. Fire severity was included in the multivariate models as a categorical variable. After fitting the multivariate models, the smoothing parameter and the number of basis functions were adjusted for some variables to ensure a good fit without overfitting. Afterwards, the number of base functions was checked with function gam.check().

To test hypothesis (3), we investigated the relationship between S and the distance, which was the most important predictor for canopy damage detectable in remote sensing analysis (Weiser et al., 2022). Additionally, the relationship between S and the NDVI at several timesteps after the eruption was investigated. The same was repeated for both C and N. In addition to the GAMs checking S, C and N against each other and the environmental variables, the C:N ratio as a common measure of nitrogen use efficiency was analysed in the same manner.

Additionally, Wilcoxon Rank Sum and Signed Rank Tests were used to check the potential differences in S, N and C levels and the C:N ratio between needle samples taken within and outside 7 km of the eruption. This threshold was chosen based on observed patterns from our previous study.

3. Results

The interpolation of the tephra layer estimated a total volume of 2.3×10^7 m^3 of tephra. The thickness of the tephra layer declines with increasing distance (Figure 2). Distance also shows a weak directional trend with slightly more tephra in the northeast and south compared to the other directions.

When fitting the GAMs, most topographic variables (elevation, TPI_{15}, TPI_{50}) showed strong concurvity with the distance to the volcano or each other and were therefore removed. Tephra depth also showed concurvity and had less explanatory power than distance. For the measured S levels, distance to the volcano was the most significant variable and mean needle length was only significant with a 0.1 threshold. The multivariate model for S explained 39.4% of the deviance (Table 3), with the univariate model using only distance as an explanatory variable explaining 31%.

Table 3: Model parameters of the multivariate generalized additive models (GAMs) explaining the content of sulphur (S), carbon (C), nitrogen (N) and the C:N ratio by different selected variables. s() marks variables where a smoothing parameter was applied. In some cases, number of base functions (k) and smoothing parameter (sp) were manually adjusted. In these cases, both are stated. The column "edf" gives the "effective degrees of freedom", representing the complexity of the smooth, with values close to 1 marking a linear, straight line and higher values a more complex smooth. The severity of the 2016 fire was included as a categorical variable.

Variable	edf	p-value	Significance
Sulphur content ~			
s(distance to volcano, k=20, sp=2)	3.321	0.0001	***
+ s(easterness)	2.329	0.2381	
+ s(slope)	1	0.1247	
+ s(mean needle length)	1	0.0672	
+ severity of the 2016 fire			
	Deviance explained	39.4%	
Carbon content ~			
s(distance to volcano, k=20, sp=2)	3.324	0.7091	
+ s(Sulphur content)	1	0.0214	*
+ s(easterness)	1	0.3483	
+ s(slope)	1	0.1822	
+ s(mean needle length)	1	0.8904	
+ severity of the 2016 fire			
	Deviance explained	28.4%	
Nitrogen content ~			
s(distance to volcano, k=20, sp=0.2)	3.318	0.4358	
+ s(Sulphur content)	1	<0.0001	***
+ s(easterness)	1	0.2109	
+ s(slope)	1	0.0185	*
+ s(mean needle length)	1.263	0.0056	**
+ severity of the 2016 fire			
	Deviance explained	42.5%	
C:N ratio ~			
s(distance to volcano, k=20, sp=0.2)	5.793	0.0459	*
+ s(Sulphur content)	1	<0.0001	***
+ s(easterness)	1	0.3821	
+ s(slope)	1	0.0333	*
+ s(mean needle length)	1.361	0.0005	***
+ severity of the 2016 fire			
	Deviance explained	48.59%	

For the C content of needles, S content was the only significant variable. The overall model explained 28.4% of the deviance (Table 3). The univariate model C ~ s(distance to volcano) explained 14.1% of the deviance (Figure 3).

For the N content of needles, in addition to S content the slope derived from the DEM and the mean length of needles were significant with the overall model explaining 42.5% of deviance (Table 3). Distance alone only explained 6.5% of the deviance (Figure 3).

The C:N ratio was significantly explained by the distance to the volcano with the S content, the slope, and the mean needle length, overall explaining 48.6% of the deviance (Table 3). In the univariate models, distance alone accounted for 14.9% of the deviance (Figure 3).

Fire severity of the 2016 wildfire was included in all models as a categorical variable. Only the level "no fire" had a significant (or in some cases significant on the 0.1 level) effect on the model.

C and S levels were significantly different for trees within 7 km to the crater compared to trees further away. For N and the C:N ratio, no significant difference was detected.

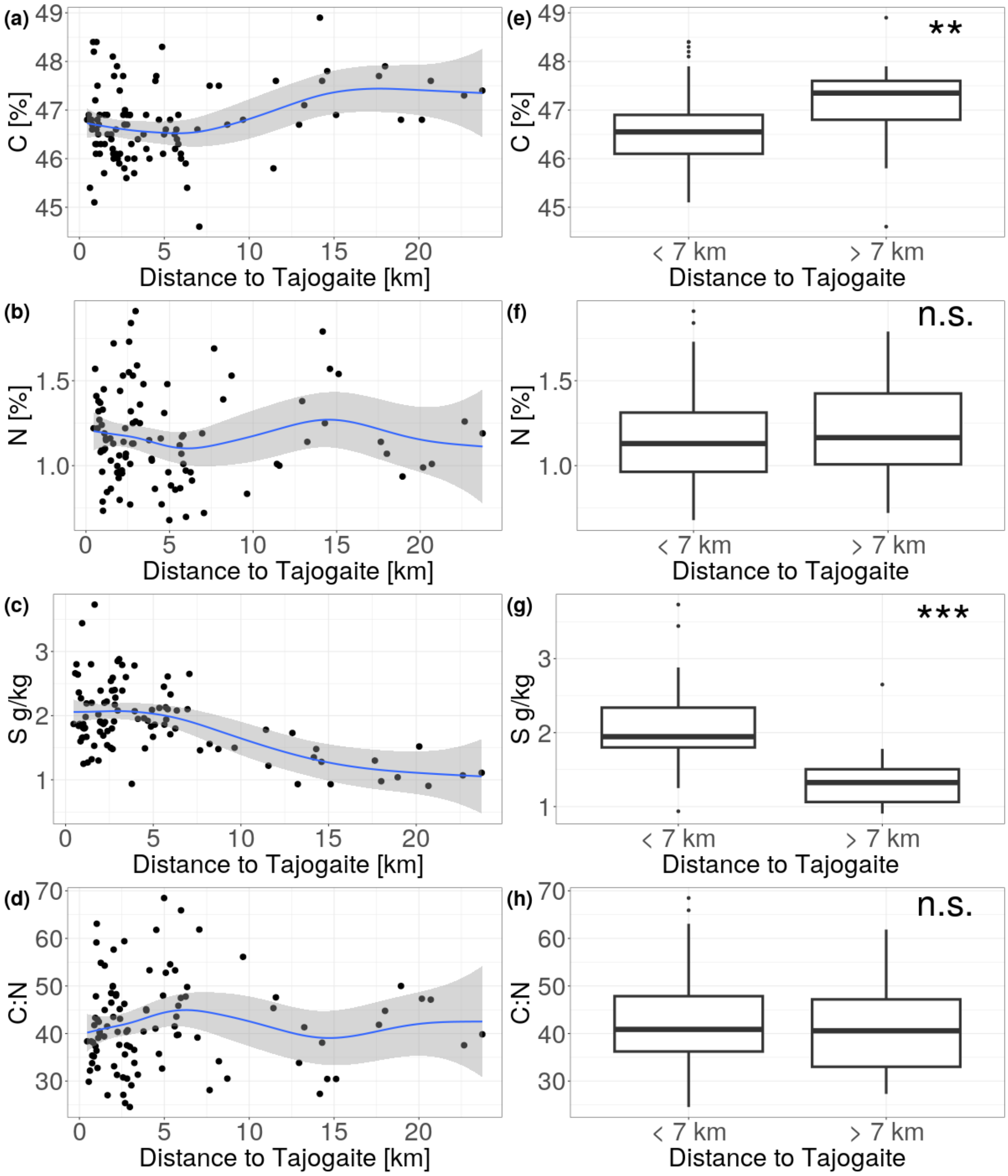

Figure 3: (a-d) show the relationship between distance to the crater of the volcano and carbon (C) content (a), nitrogen (N) content (b), sulphur (S) content (c) and C:N ratio (d). The blue line represents the fitted generalized additive models (GAMs) with the 95% confidence interval, explaining a) 14.1%, b) 6.5%, c) 31%, and d) 14.9% of the Deviance. The boxplots show C content (e), N content (f), S content (g) and C:N ratio (h) of the 80 needles samples closer than 7 km to the crater (left) compared to those further away (right). Wilcoxon tests showed significant differences between the two samples for both C (p-value = 0.00219) and S (p-value <0.0001), but not N (p-value = 0.37) and C:N ratio (p-value = 0.496).

S explained 18.2% of the deviance in the C contents (Figure 4, Table A1), 13.3% for N and 10.3% for the C:N ratio. N explained 16.3% of the variance in the C content.

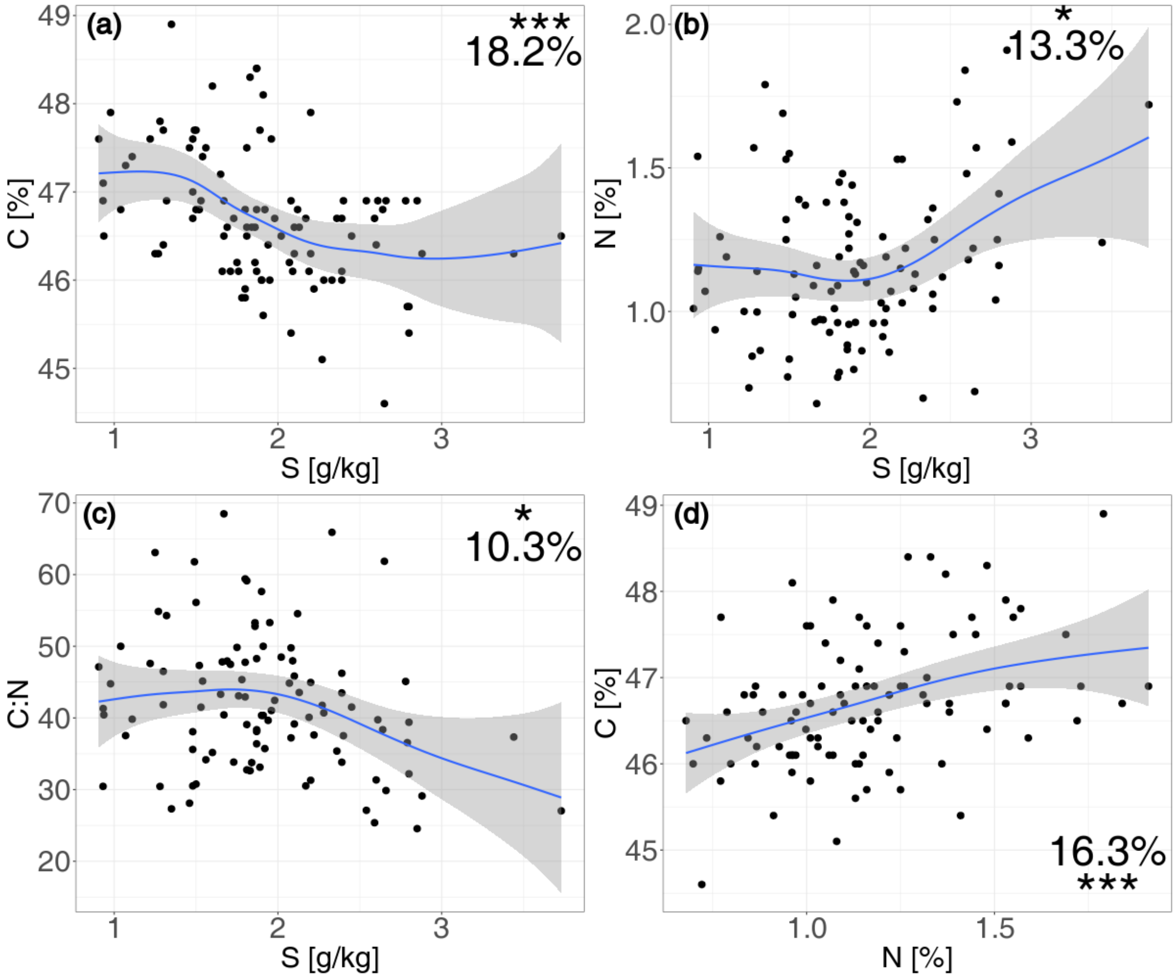

Figure 4: The relationship between a) carbon (C) and sulphur (S) b) nitrogen (N) and S c) C:N ratio and S and d) C and N. The blue lines represent a generalized additive model (GAM) of the formula y~ s(x) with y and x being the two modelled elements and s the smoothing parameter. For exact model parameters, see Table A1. The grey boundaries show the 95% confidence interval of the model. Significance of the variables is shown in the top right (bottom right for d) corner. Explained deviance was (a) 18.2%, (b) 13.3%, (c) 10.3 % and (d) 16.3%.

The NDVI difference for pixels where we took needle samples shows a clear distance-based damage pattern (see also Weiser et al., 2022) up until the image taken 8 months after the end of the eruption (Figure 5). One year after the eruption, the NDVI for the majority of pixels has returned to the same level as 2019 or higher. A few pixels still show negative or strongly negative NDVI changes. The NDVI difference of pixels corresponding to our sampled trees did not show any significant correlations to measured S, N or C content (Figure A1, A2 and A3).

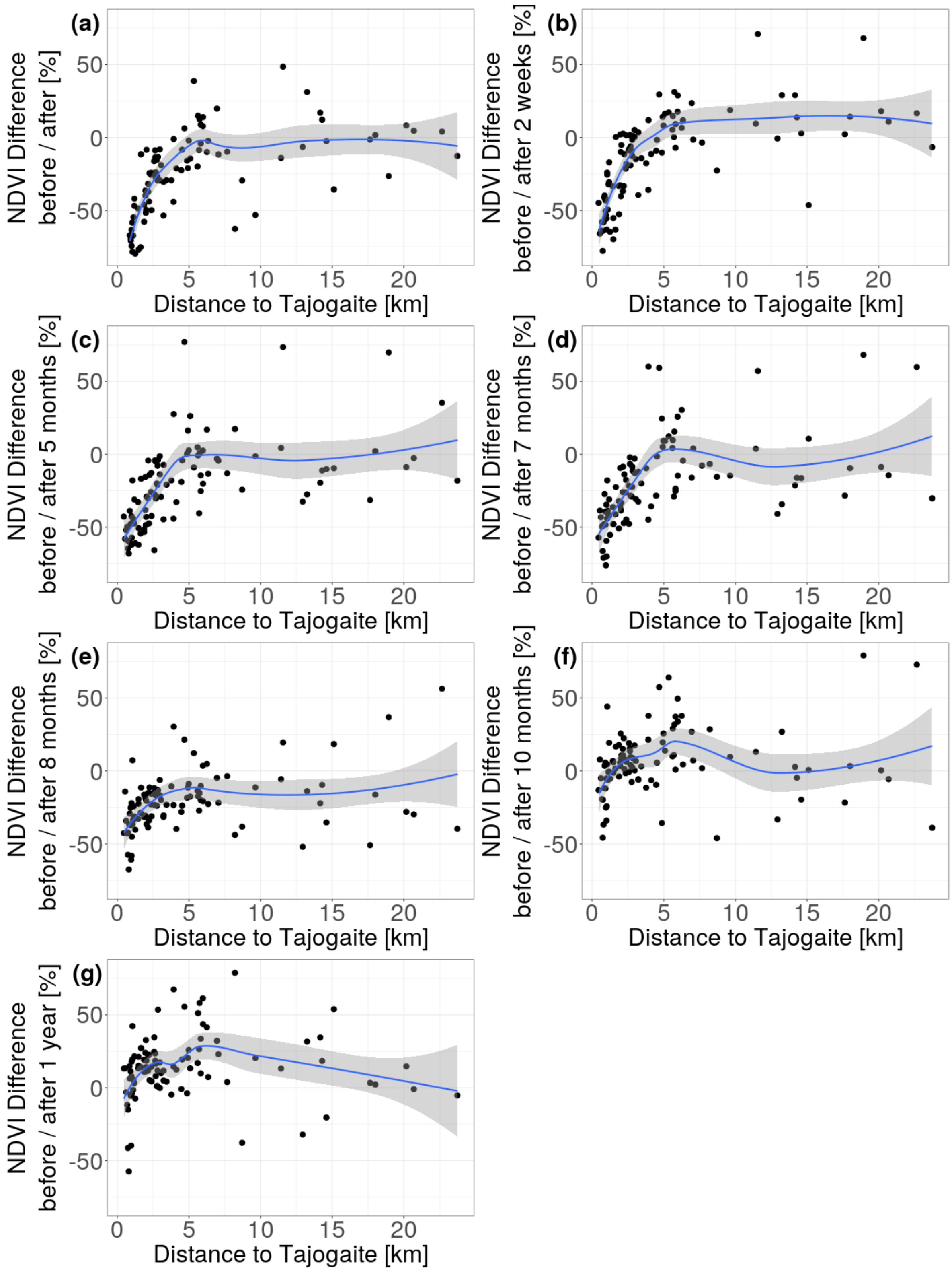

Figure 5: Normalized Difference Vegetation Index (NDVI) Difference for different timeframes plotted against the distance to the eruption. NDVI Difference was calculated for a cloud-free image before the eruption (2019-11-30) and (a) directly after, (b) 2 weeks after, (c) 5 months after, (d) 7 after, (e) 8 months after, (f) 10 months after and (g) 1 year after the end of the eruption. Exact image dates can be found in Table 1.

When cropped to a distance of 7 km, based on the observations from our previous remote sensing based study (Weiser et al. 2022), NDVI values initially show a similar pattern with damage reaching up to 7 km. In the months after the eruption, the majority of damage occurs within the first 3 km of the volcanic crater (Figure 6)

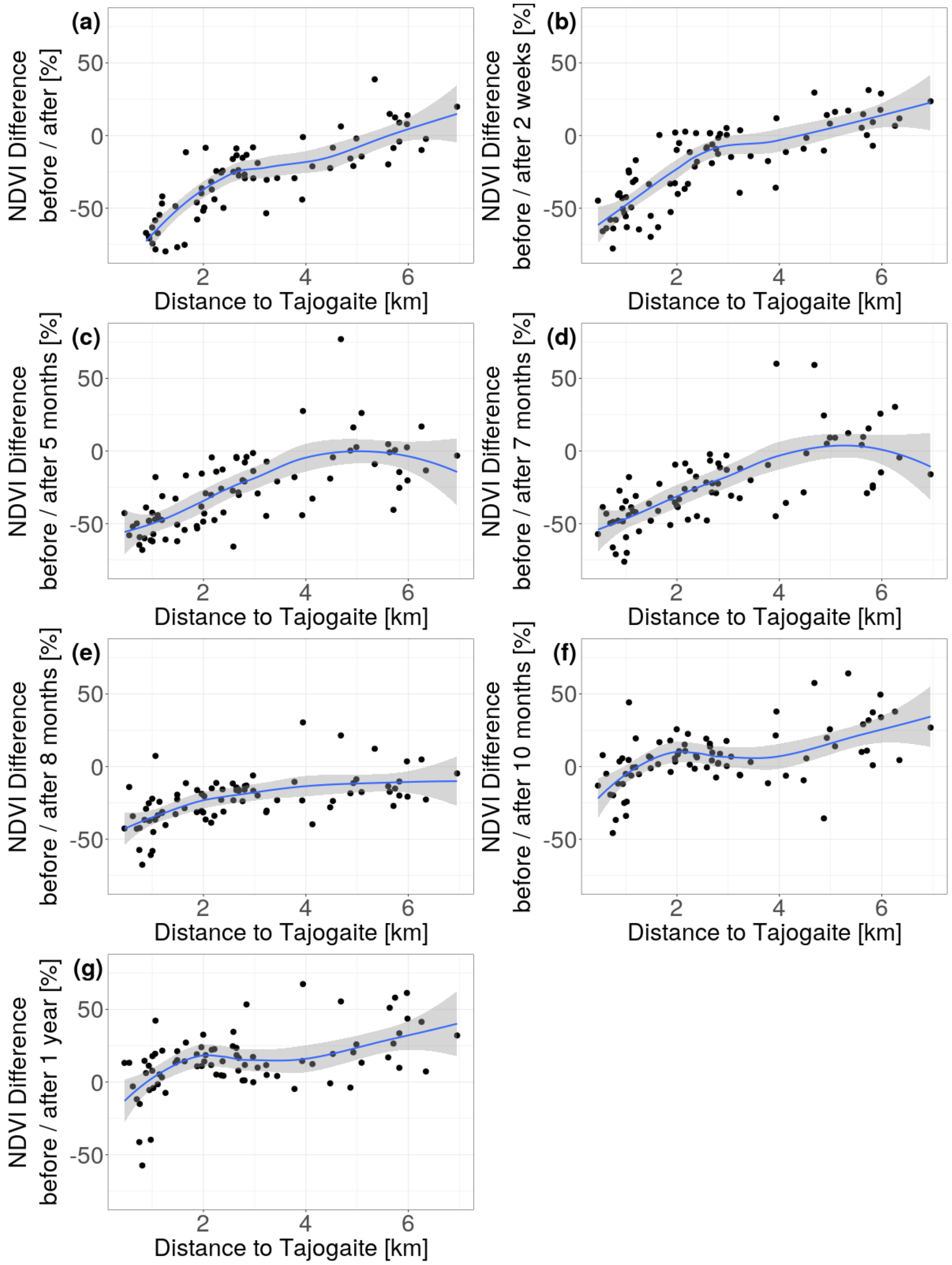

Figure 6: Normalized Difference Vegetation Index (NDVI) Difference for different timeframes plotted against the distance to the eruption for the first 7 km. NDVI Difference was calculated for a cloud-free image before the eruption (2019-11-30) and (a) directly after, (b) 2 weeks after, (c) 5 months after, (d) 7 months after, (e) 8 months after, (f) 10 months after and (g) 1 year after the end of the eruption. Exact image dates can be found in Table 1.

4. Discussion

Overall, we found the expected strong influence of distance to the volcanic eruption crater for needle S content, with higher S levels closer to the eruption. This is not surprising given the high amount of at least 1Tg SO_2 emitted during the eruption (IGME, 2022). Additionally, the volcanic vents emitted and still emit gases for a long time after the eruption. In the post eruptive phase, SO_2 emissions declined from 670 Mg per day to 219 Mg one month after the end, 107 Mg three months after and 13 Mg per day in April 2022 (Rodríguez et al., 2023). Recent measurements show an emission of 2-3 Mg per day in April 2023 (Nemesio Pérez, personal communication, April 21, 2023). Needle S content measured in this study fit values found in the literature for *P. canariensis* in trees far away from the eruption and in some individuals found closer, while the majority of sampled trees close to the crater exhibited S levels up to three times higher than reported normal values (Tausz et al., 2005)

The threshold of canopy damage visible for up to ~7 km found in our previous remote sensing-based study (Weiser et al., 2022) is also visible in our needle samples, with significant differences in S and C but not N and C:N ratio. We expected topography to influence these measured levels, with trees situated in depressions being more protected from acidic gases compared to their surroundings. However, we did not find a strong influence of topography on S levels, presumably due to more than half of days with no trade wind influence causing the volcanic gases to spread in all directions instead of being blown out to sea. The plume also reached an average height of 3.5 km (Felpeto et al., 2022 as reported in Bonadonna et al., 2022), spreading out during its rise and distributing SO_2 all over the island and even to Tenerife (Milford et al., 2023), likely making local variations in topography irrelevant.

For C, N and C:N ratio, the S levels were an important predictor. High S content in the needles led to a decrease in C, an increase in N and subsequently a decrease in the C:N ratio. While the reasons for this relationship are not clear, the likely reason for the C decrease is the mobilization of C associated with resprouting in *P.canariensis* (Miranda et al., 2020). The increase in N at higher S levels was contrary to our expectations, which predicted a loss of N caused by chlorotic damage, similar to the decrease after a fire. We identified possible explanations for this pattern: There is a visible yet insignificant difference in N levels between trees within and outside of the burnt area of the 2016 wildfire, this area being within the 7 km radius around the eruption. Trees within the burnt area have an average N content of 1.09% and those outside 1.25%, with Canary Pine needle N commonly decreasing after fire (Durán et al., 2010). A group of samples close to the Refugio El Pilar, approximately 2.5 km east of the volcano, had both very high N levels with high S values. These trees are situated in a climatically favourable position in a depression on the saddle between Cumbre Vieja and Cumbre Nueva and were left unburnt in 2016. This may explain their very high N content, which is at the same level as the N content of the control samples far away from the eruption. These trees are also only ca. 2.5 km away from the eruption, causing high S needle levels. This group of samples is therefore highly influential in our model and suggests why high S content is correlated with high N content. This effect is even more pronounced when the relationship is modelled for only the first 7 km, which removes the control trees with high N but low S content far away from the volcano.

The observed pattern of C, N, and C:N levels was less clear than expected, with levels close to the crater varying strongly between trees. In some cases, C levels were higher than control trees far away from the eruption. Nonetheless, this is in line with the findings of Miranda et al. (2020), who simulated both defoliation and damage to *P. canariensis* and measured, among other variables, non-structural carbohydrate levels in needles. In their study, soluble sugar showed little difference between control and damaged trees while needle starch content only differed strongly in the following growing season, as needles from defoliated and damaged trees varied much more than control trees.

Interpolating the tephra blanket from our field measurements and the freely available UAV based DSM (Civico et al., 2022) worked well. The resulting total volume of the tephra layer was 2.3 x 10^7 m^3, which is very well in line with the values reported by Bonadonna et al. (2022) based on more sophisticated models. The directional patterns can be explained by the dominant wind direction caused by the trade winds, which blew from the north-east for roughly half of the days during the eruption (Bonadonna et al., 2022). During the other days, trade winds were weak or not blowing, causing the omnidirectional distribution of ash and gases, and weakening the northeast to southwest pattern of the tephra layer. Additionally, the ridge of Cumbre Vieja, which is approximately 500 meters higher than the Cumbre Nueva, shields the south-eastern part of the island from tephra depositions. Even given the significant S content of both ash (Delmelle et al., 2005) and tephra (Zobel & Antos, 1991; Ayris & Delmelle, 2012), we did not find a significant effect of tephra and ash depth on needle composition. Given the strong concurvity and correlation between tephra and ash depth itself and distance to the eruption, tephra and ash depth was excluded from the GAMs. Even when included, it added little to the explained variance. Tephra depth likely contributes little to the explanatory power of the models that is not already covered by volcanic distance. The direct deposits of volcanic gases had a stronger effect than tephra S content, presumably because leaching processes can take several months to years (Zobel & Antos, 1991). *Pinus canariensis* has been subject to volcanic eruptions for millions of years and is often a colonizer of recent volcanic tephra blankets (Lopéz et al., 2013) making it likely that the species is well adapted to soluble compounds in fresh tephra. Other effects, such as moisture within the tephra blanket affecting the stem are possibly minor or only affect individual trees later.

Overall, the S levels in needles of trees close to the eruption reflect the immense levels of volcanic gases, e.g. more than 1 Tg of SO_2 that affected these trees and caused the chlorotic damage visible in the canopy for the months following the eruption. Levels were up to three times higher than literature values (Tausz et al., 2005). The decrease in C indicates the energy expended for the visibly extensive resprouting of the affected trees. The high variation in levels of S, C and N in *P. canariensis* needles close to the crater is likely caused by plant physiological processes and strongly depends on resprouting. Large amounts of C are often needed to resprout (Clarke et al., 2013). The amount of resprouting happening varied for the sampled trees. Additionally, by the time of our sampling five months after the end of the eruption, some of the trees in the area had already resprouted up to three times (Personal observation, Figure 7).

Figure 7: Resprouting *Pinus Canariensis* (Photograph: Anke Jentsch)

While the change in the NDVI indicates that the chlorotic damage suffered by trees lasted several months, after one year most of the forest canopy has recovered (Figure 5 and 6). In most pixels, the NDVI is even higher than in 2019, when the canopy was still in recovery after the 2016 wildfire. *Pinus canariensis* is very resilient and recovers quickly from fire but nonetheless may take several years to reach a full canopy again. Only eight sampled forest pixels still show a negative NDVI change larger than 10% one year after the eruption, indicating full recovery of most pixels.

This is in line with patterns observed in the true colour Sentinel-2 images, where large scale browning of the canopy is visible 5 months after the eruption. One year after the eruption, most of the forest canopy is green again, with trees close to the crater still brown or dead. This pattern is not linked with the S, C or N levels measured.

The missing link between NDVI change and S, N or C content (Figure A1, A2 and A3) can be explained by differences in what is being measured. Chlorotic damage starts at the tip of the needle, moving toward the stem (Knabe, 1976). At first glimpse, most affected trees around the crater showed a similar level of browning and senescence. Up close, differences became apparent. In some cases, most of the needle tissue was dead and little to no resprouting had happened yet. In other cases, the outward appearance of senescent needles was deceptive, and more than half of each needle was still green and photosynthetically active. This would mean that C was still assimilating in the needle. In satellite imagery, where only the exposed top of the canopy is visible, this difference is presumably not reflected since the outward facing tissue is more important for the calculated NDVI values. Differences in resprouting also means that trees with similar levels of canopy damage and NDVI change in the Sentinel-2 images might have very different nutrient levels in their needles.

Newer satellite images one-year post-eruption show that the canopy of most of the Canary Pine forest is green apart from the immediate surroundings of the crater. However, the craters are still emitting SO_2 (Rodriguez et al., 2023) and a directional pattern of damage, which will be the subject of follow up studies, is visible. The recovery shows the extraordinary resilience of *P. canariensis*, which has been present on the Canary Islands for at least 13 million years (Casañas et al., 1995). During this time, the species has evolved under frequent volcanic eruptions and is therefore well adapted to their survival (López de Heredia et al., 2014). There is even evidence that the species survived the "Roque Nublo" period on nearby Gran Canaria (Anderson et al., 2009), where volcanism was so violent, that a *de facto* sterilization of the island has been hypothesized (Emerson, 2003). Another study showed that *P. canariensis* was able to survive sustained wounds and strongly elevated mercury levels during the 1949 San Juan eruption (Rodríguez Martín et al., 2013). We therefore expect most sampled trees to make a full recovery from the sustained damage and very high levels in S.

5. Conclusion

In conclusion, our study provides valuable insights into the changing chemical composition / leaf nutrients in needles of *Pinus canariensis*. While S exhibited the clear distance-influenced pattern we expected, only C followed a similar pattern, showing a clear link between suffered chlorotic damage and C usage for damage repair and resprouting. Both C and N levels were strongly but antagonistically influenced by S levels of needles. Overall, the patterns detected were less clear with high variation close to the crater and no relation between needle nutrient status and canopy NDVI at different timesteps was detected. Resprouting of trees had a strong effect on C, N and S, which is not explained by the variables we measured. Additionally, our study provides only one single snapshot of needle nutrient status within one year after the eruption. To clearly understand the recovery (or lack thereof, as many of the affected trees might not recover) of *P. canariensis*, more sampling and close observation of the mid- and long-term recovery dynamics after the volcanic eruption is necessary.

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Author contributions:

Frank Weiser: Conceptualization, Methodology, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Funding acquisition **Anna Walentowitz:** Conceptualization, Methodology, Formal analysis, Investigation, Writing - Original Draft, Visualization, Funding acquisition **Esther Baumann:** Writing - Original Draft, Writing - Review & Editing **Christopher Shatto:** Writing - Original Draft, Formal analysis, Writing - Review & Editing **María Guerrero-Campos:** Writing - Review & Editing **Anke Jentsch:** Investigation, Writing - Review & Editing, Funding acquisition **Manuel Nogales:** Writing - Review & Editing **Félix Manuel Medina:** Writing - Review & Editing **Ole R. Vetaas:** Writing - Review & Editing **Carl Beierkuhnlein:** Conceptualization, Methodology, Writing - Original Draft, Writing - Review & Editing, Supervision, Project administration, Funding acquisition

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Appendix

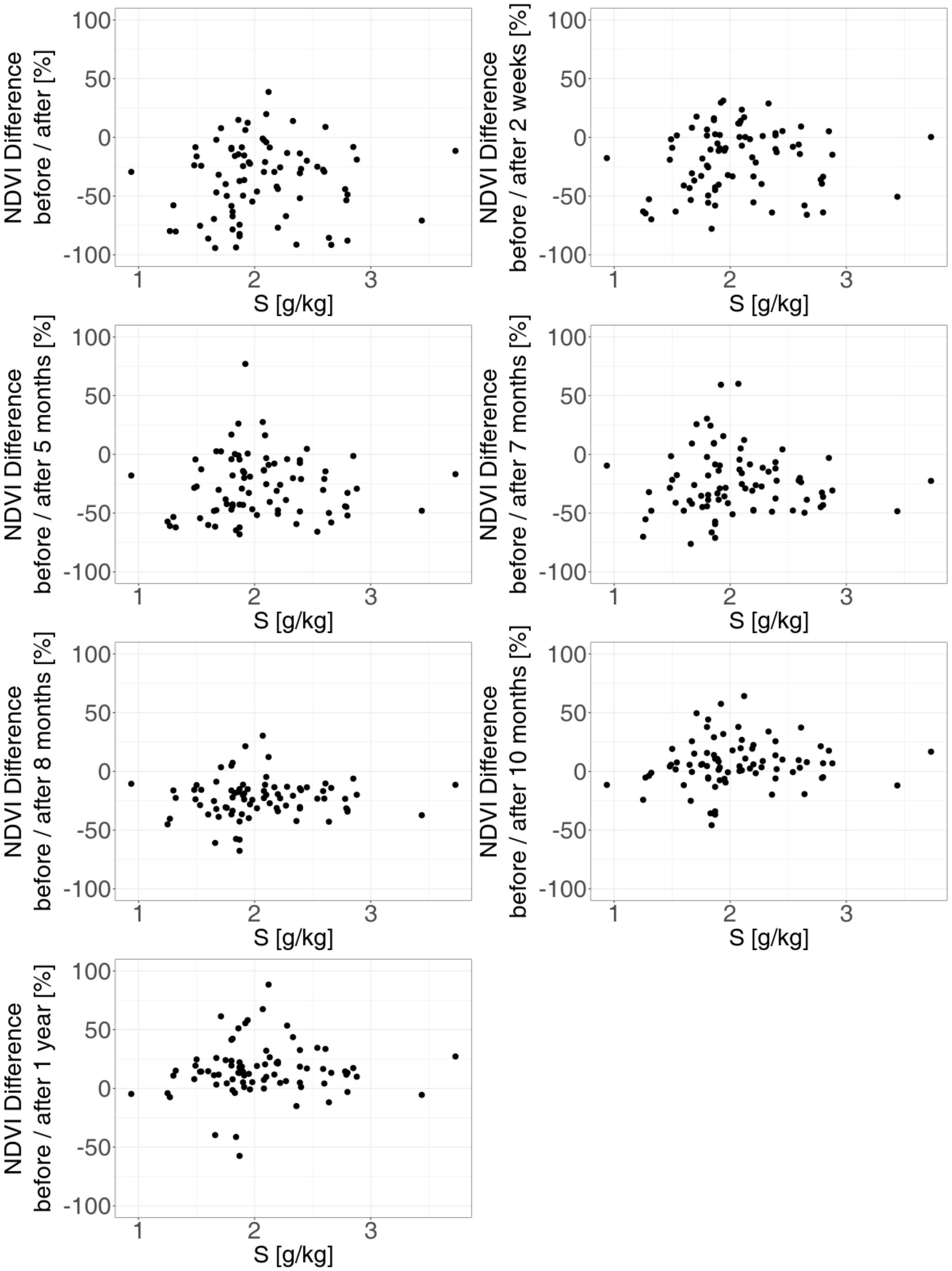

Figure A1: Normalized Difference Vegetation Index (NDVI) difference against sulphur (S) levels measured in our needle samples for the first 7 kilometres from the volcano. The NDVI Difference was calculated between an image before the eruption (30th of November, 2019) and several timesteps after the eruption. The exact image dates can be found in Table 1.

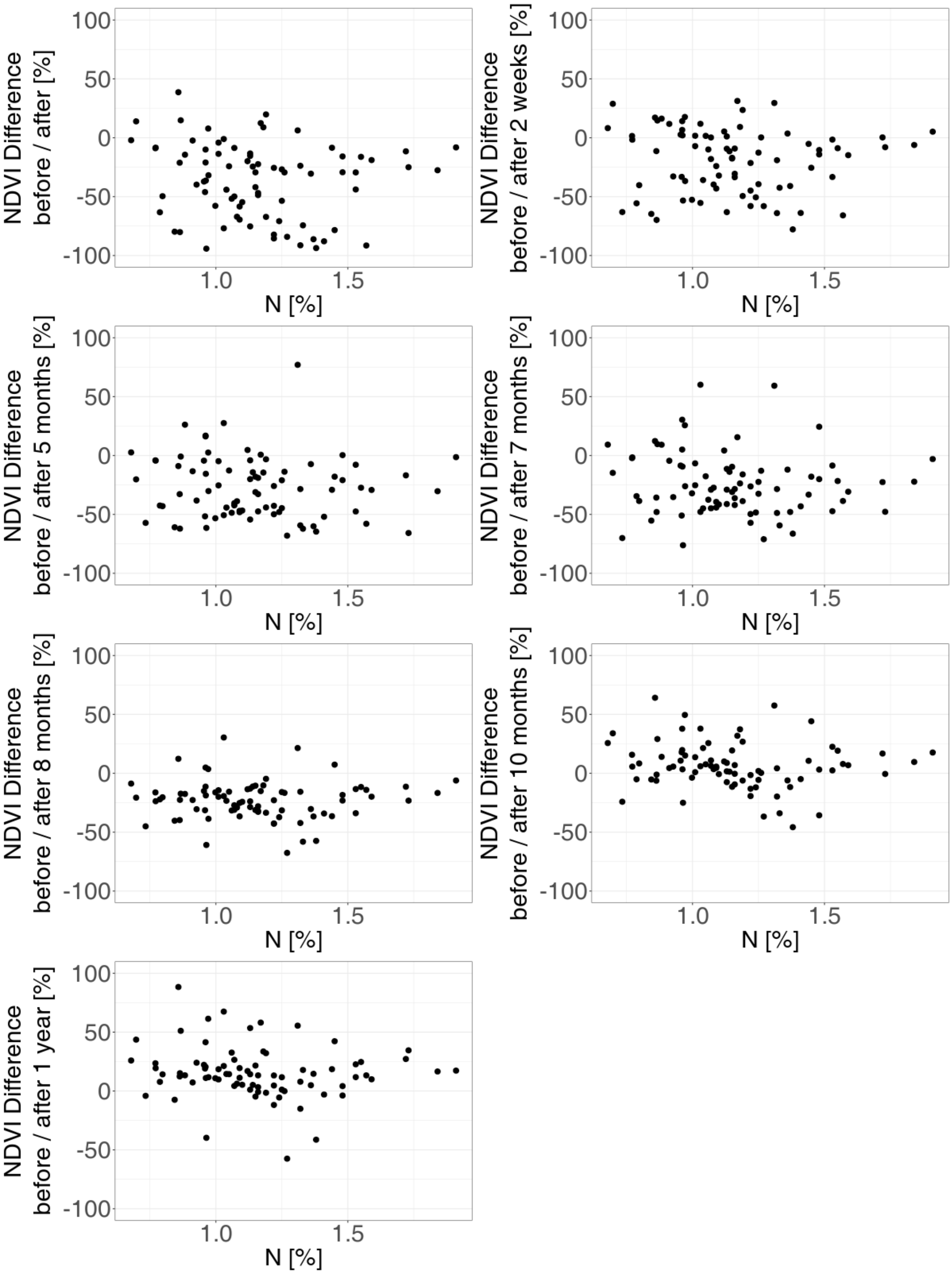

Figure A2: Normalized Difference Vegetation Index (NDVI) difference against nitrogen (N) levels measured in our needle samples for the first 7 kilometres from the volcano. The NDVI Difference was calculated between an image before the eruption (30th of November, 2019) and several timesteps after the eruption. The exact image dates can be found in Table 1.

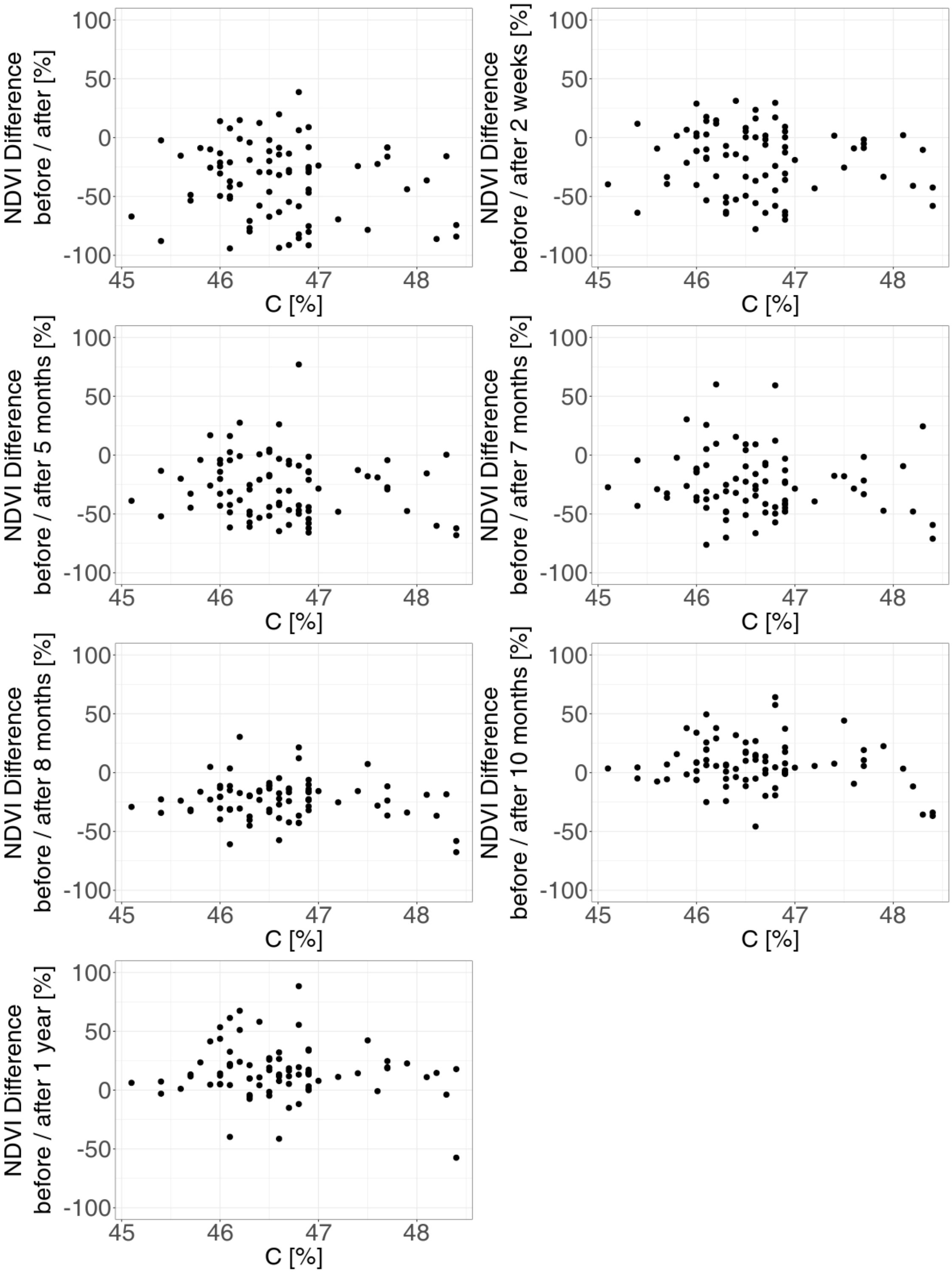

Figure A3: Normalized Difference Vegetation Index (NDVI) difference against carbon (C) levels measured in our needle samples for the first 7 kilometres from the volcano. The NDVI Difference was calculated between an image before the eruption (30th of November, 2019) and several timesteps after the eruption. The exact image dates can be found in Table 1.

Table A1: Generalized Additive Model (GAM) coefficients of needle carbon (C), nitrogen (N) and C:N ratio explained by sulphur (S) as well as C against N. edf = effective degrees of freedom, k= number of basis functions, sp= smoothing parameter

Variable	edf	p-value	Significance
Carbon content ~ s(Sulphur, k=10, sp=1)	2.276	<0.0001	***
	Deviance explained	18.2%	
Nitrogen content ~ s(Sulphur, k=15, sp=3)	3.51	<0.0001	***
	Deviance explained	13.3%	
C:N ratio ~ s(Sulphur, k=15, sp=3)	3.269	0.0435	*
	Deviance explained	10.3%	
Carbon content ~ s(Nitrogen, k= 15, sp=3)	2.782	<0.0001	***
	Deviance explained	16.3%	

6.4 Manuscript 4

Castanea sativa (leafless trees) on the eastern slopes of La Palma

Assessing the Potential Replacement of Laurel Forest by a Novel Ecosystem in the Steep Terrain of an Oceanic Island

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Authors: Ram Sharan Devkota [1], Richard Field [2], Samuel Hoffmann [1], Anna Walentowitz [1], Félix Manuel Medina [3,4], Ole Reidar Vetaas [5], Alessandro Chiarucci [6], Frank Weiser [1], Anke Jentsch [7,8] and Carl Beierkuhnlein [1,8,9,*]

Affiliations:

[1] Department of Biogeography, University of Bayreuth, Universitätsstraße 30, 95447 Bayreuth, Germany;

[2] School of Geography, University of Nottingham, Nottingham NG7 2RD, UK;

[3] Servicio de Medio Ambiente, Cabildo de La Palma, 38700 Santa Cruz de La Palma, Spain;

[4] Ecology and Evolution Research Group, Instituto de Productos Naturales y Agrobiología (IPNA-CSIC), 38206 San Cristóbal de La Laguna, Spain

[5] Department of Geography, University of Bergen, P.O. Box 7802, 5020 Bergen, Norway;

[6] Biodiversity and Macroecology Group, Department of Biological, Geological & Environmental Sciences, Alma Mater Studiorum-University of Bologna, Via Irnerio 33, 40126 Bologna, Italy;

[7] Disturbance Ecology, University of Bayreuth, D-95440 Bayreuth, Germany;

[8] Bayreuth Center for Ecology and Environmental Research BayCEER, D-95440 Bayreuth, Germany

[9] Geographical Institute Bayreuth GIB, D-95440 Bayreuth, Germany

* **Correspondence**: carl.beierkuhnlein@uni-bayreuth.de

Abstract

Biological invasions are a major global threat to biodiversity and often affect ecosystem services negatively. They are particularly problematic on oceanic islands where there are many narrow-ranged endemic species, and the biota may be very susceptible to invasion. Quantifying and mapping invasion processes are important steps for management and control but are challenging with the limited resources typically available and particularly difficult to implement on oceanic islands with very steep terrain. Remote sensing may provide an excellent solution in circumstances where the invading species can be reliably detected from imagery. We here develop a method to map the distribution of the alien chestnut (*Castanea sativa* Mill.) on the island of La Palma (Canary Islands, Spain), using freely available satellite images. On La Palma, the chestnut invasion threatens the iconic laurel forest, which has survived since the Tertiary period in the favourable climatic conditions of mountainous islands in the trade wind zone. We detect chestnut presence by taking advantage of the distinctive phenology of this alien tree, which retains its deciduousness while the native vegetation is evergreen. Using both Landsat 8 and Sentinel-2 (parallel analyses), we obtained images in two seasons (chestnuts leafless and in-leaf, respectively) and performed image regression to detect pixels changing from leafless to in-leaf chestnuts. We then applied supervised classification using Random Forest to map the present-day occurrence of the chestnut. Finally, we performed species distribution modelling to map the habitat suitability for chestnut on La Palma, to estimate which areas are prone to further invasion. Our results indicate that chestnuts occupy 1.2% of the total area of natural ecosystems on La Palma, with a further 12–17% representing suitable habitat that is not yet occupied. This enables targeted control measures with potential to successfully manage the invasion, given the relatively long generation time of the chestnut. Our method also enables research on the spread of the species since the earliest Landsat images.

Keywords: invasive species; island ecology; assisted migration; laurel forest; plant functional type; deciduous trees; species distribution models; Landsat 8; Sentinel-2; *Castanea sativa*

1. Introduction

Oceanic islands play an eminent role in speciation and endemism [1], and they contribute disproportionately to global biodiversity relative to their small area [2]. Their isolation, aggregation in archipelagos, island life cycles, relief dynamics, climate, topography, and natural and anthropogenic disturbance regimes produce and maintain a high diversity of biota and the respective ecosystems formed by those species [3]. Oceanic islands are often seen as evolutionary showcases [4] prone to pulse dynamics [5] or as evolutionary arenas [6], where speciation can be studied. However, the uniqueness of their flora, fauna, and ecosystems is also related to the fact that they host relict species and ecosystems, such as the evergreen laurel forest in the Canary Islands including our study region: the entire island of La Palma [7].

Endemic ecosystems (i.e., specific ecosystems that are characterized and dominated by species with a very limited spatial distribution) are particularly threatened by species invasion [8–11]. Invasive species are species that establish in new, non-historical ranges and are harmful to their environment [12]. They can decrease native species abundances via competition, predation, parasitism, and alteration of habitat conditions, causing a loss of biodiversity, ecosystem functioning, and services [13]. Invasive species often cause huge economic costs for society [14]. The abundance of invasive species was recently found to have increased by up to 70% across 21 countries since 1970 [15]. The focus of invasion research is mostly on prominent single species of well-known invasion potential, such as *Lantana camara* or *Ailanthus altissima* [16,17]. Non-native woody species are disproportionately represented among the most severe invaders around the world [18], and escapes of tree species from plantations have been highlighted as a particular problem [19]. Chestnut (*Castanea sativa* Mill.) (Fagaceae) is a widespread deciduous tree species across Europe, often managed for fruit and wood production. It is also an important species for apiculture and historically has had other uses such as in tanning and pig farming [20]. The species was introduced to La Palma as early as 1493 [21] and managed in orchards, most of which are abandoned today. Observations of local authorities suggest that the species is increasingly establishing in natural, evergreen forest ecosystems—*C. sativa* is the agent of change in the ongoing replacement of a native ecosystem by an ecosystem that did not previously exist on La Palma. Such a deciduous broadleaved forest, with pronounced seasonal leaf phenology, is a novel ecosystem in the context of the Canary Islands. Remote sensing (hereafter abbreviated to RS) has been used for almost 65 years in vegetation science [22]. However, ecological studies from space only began after the launch of Landsat 1 in 1972 [23]. In many cases, RS is the only feasible method for measuring the characteristics of habitats across broad areas and for detecting environmental changes that occur as a result of human or natural processes [24]. It is becoming increasingly popular among conservationists and ecologists. Satellite-based data have a wide range of applications in ecological studies, including mapping of plant communities and also single plant species [25]. A recent study on La Palma used a time series of Sentinel-2 images to identify plant communities and measure beta-diversity [26].

Remote sensing is advancing invasion research and management by detecting and mapping invasive species, their drivers, and potential future distributions [27,28]. Differences in structural, biochemical, and physiological characteristics between species can make it possible to distinguish invasive plant species from native co-occurring vegetation by their spectral signatures [29]. However, there are limits to this if invasives and natives share comparable reflection spectra. If phenological differences between species exist, these can play a key role in identifying invasive species within native vegetation by RS [30]. To detect seasonal phenological differences between plant species, multitemporal RS data are required, for instance, provided by spaceborne Landsat and Sentinel sensors. The timing of RS acquisition is crucial for the detection of phenologically differentiated species. Accordingly, Evangelista et al. [31] used six Landsat 7 ETM+ satellite scenes across the growing season to remotely sense the evergreen *Tamarix* species invading native deciduous vegetation along the Arkansas River in Colorado, USA.

Slight differences in seasonal phenology can be sufficient to monitor invasive plant species but may require hyperspectral airborne sensors to detect them, with the trade-off of high costs [32]. Such hyperspectral approaches and time series can help to identify invasive plant species even in non-seasonal climate and ecosystems, as demonstrated by Asner et al. [33], who detected the invasive evergreen shrub *Myrica faya* Dryand. (syn. *Morella faya* Aiton) in Hawaiian rainforests. However, that study used EO-1 Hyperion satellite data, and this satellite (and sensor) has been decommissioned and is no longer available.

Generally, the potential to detect invasive species remotely increases with finer spectral, spatial, and temporal resolution of RS imagery [34]. Tarantino et al. [17] showed the potential of multi-seasonal panchromatic WorldView-2 satellite imagery for mapping the deciduous tree *Ailanthus altissima* (Mill.) Swingle, invading a protected area in Southern Italy. In this case, the detection of the invasive tree species was enhanced by the contrast with the grass cover of the invaded ecosystems, as well as the multitemporal, multispectral, and very high-resolution satellite imagery. Even if there is a follow-up satellite (WorldView-3) after the soon-expected end of the lifetime of WorldView-2, the data are not freely accessible, limiting their use for conservation practice and for comparative studies. Free and open-access RS data provide unlimited use but come at the expense of relatively coarse spatial, spectral, and temporal resolution.

Remote sensing also supports invasion research and management indirectly by providing RS data for species distribution and habitat suitability models [27,30]. Vicente et al. [35] were able to map the current and predict the future distribution of the invasive tree species *Acacia dealbata* Link in northern Portugal using remotely sensed predictor variables. In contrast to species distribution models, ecological niche modelling and habitat suitability mapping aim to reveal the potential distribution of a species by applying interpolation between known species occurrences. Such modelling techniques and resulting maps aim to guide conservation management and planning [36]. Andrew and Ustin [37] modelled the habitat suitability of the noxious pepperweed (*Lepidium latifolium* L.) invading San Francisco Bay/Sacramento-San Joaquin River Delta, California, USA. Species presence was derived from airborne HyMap hyperspectral imagery and environmental predictors from LiDAR. Accordingly, RS-based modelling approaches can map and predict rapid range expansions of invasive species by monitoring invasive species' ecological niches [38].

The free availability and global coverage of RS data are beneficial for comparative studies, and for improving the quality of other study outcomes. Result validation and quality control are particularly important for studies of moving targets with enormous impact potential, such as invasive species. Based on the known benefits and limits of RS applications in invasion research, and considering options for compatibility with future studies, we use multitemporal and multispectral Landsat 8 and Sentinel-2 satellite imagery combined with field observations of *C. sativa* to investigate the current and potential future distribution of the species on the Canary island of La Palma. We used linear image regression [39] and random forest classification [40] to detect *C. sativa* and map its current spatial distribution. As the very steep and unstable slopes limit the extent of field surveys on La Palma, we utilized *C. sativa*'s distinctive phenology to map its current spatial distribution through RS. We then conducted and compared ecological niche models (hereafter ENM), also known as habitat suitability models, based on field observations of *C. sativa* and on remotely sensed *C. sativa* occurrences. This study thus aims to detect and map the invasive alien chestnut tree *C. sativa* on the island of La Palma and to assess the risk of the species replacing native and unique ecosystems such as the evergreen laurel forest of the Canary Islands.

We build on previous studies on the detection of invasive plant species through RS, aiming to improve RS-based assessments of invasive plant species not only through comparing the sensitivity of commonly used sensors that offer open RS data (Landsat/Sentinel) but also, and particularly, throughlinking modelling approaches with RS and with field data. This approach also allows better assessment of existing invasions using long time series. Additionally, we identify new potential for future invasion research. Combining RS and SDMs can provide testable predictions for future invasion processes under climate change. Finally, our study is the first using RS for a better understanding of tree invasion and its consequential impact on the unique laurel forest.

2. Materials and Methods

2.1. Study Site and Field Data

La Palma, also known as "la isla verde" or "la isla bonita", is one of the highest and westernmost islands of the Canary Islands archipelago. Large surfaces of the island are still covered by natural and semi-natural vegetation. The steep slopes in the northeast of the island are exposed to constant moisture supply by trade winds. Here, natural laurel forests are found on steep, almost inaccessible slopes (Figure 1). This ecosystem covered large parts of the northern hemisphere during the Tertiary period, as indicated by fossil records of preserved tree leaves in lignite all over Europe [41]. Today, comparable climatic conditions to the zonal climate of the Miocene (i.e., constant moisture supply and warm temperatures) exist on some oceanic islands of sufficient elevation in the trade-wind zone, including La Palma.

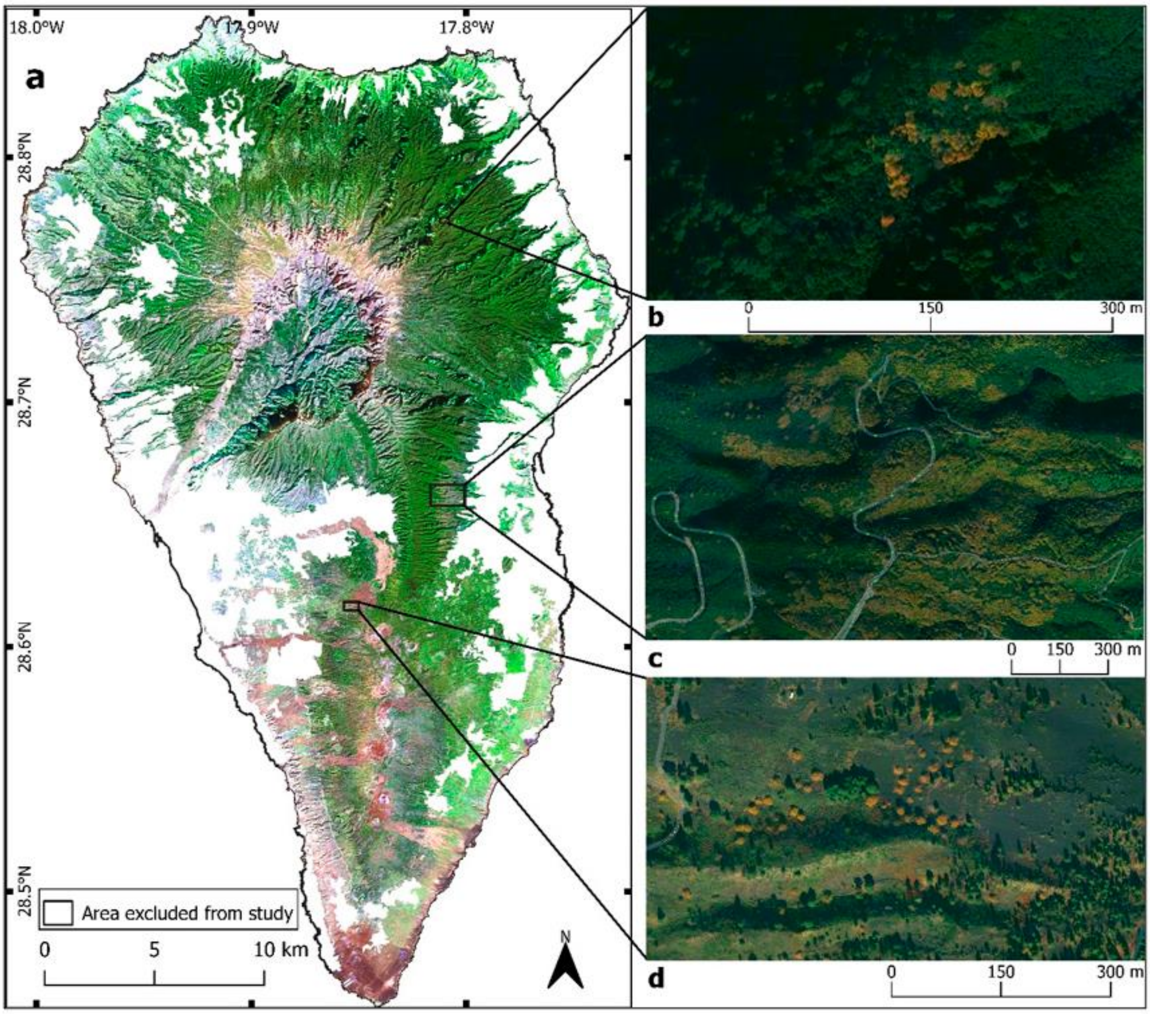

Figure 1. (**a**) Sentinel-2 true natural colour image of the study area (Red: band 4, Green: band 3, Blue: band 2). (**b–d**) are Google satellite zooms of characteristic landscape units. Trees with yellow canopy in the boxes (**b–d**) represent single trees, groups or patches of *C. sativa*.

Despite the strong resemblance in the climate, vegetation structure, and characteristic laurophyllous plant functional types between the present-day Canary Islands and the Tertiary period, the current Canary Island laurel forest is not a simple copy of a Tertiary biome. The current laurel forest species composition of the Canaries that established since the Pliocene is an assemblage of taxa that differ in origin [42]. Very likely, oceanic islands that have since eroded to guyots (seamounts) served as stepping-stones of suitable habitat for species dispersal closer to the European continent [43]. However, the laurel forest of the Canary Islands has been strongly reduced through exploitation since the European colonization [44]. Most remnant areas are on steep slopes, where access for forestry is restricted, if not impossible—but this restriction also applies to scientific field work. In consequence, RS approaches, although themselves not free from limitations associated with steepness and cloudiness, need to be implemented for data collection within and across steep valleys, slopes, and remote ridges. In situ recording of mature individuals of *C. sativa* in the field was conducted during 10–24 April 2019. We mapped individual trees, recording GPS points for each. The sampling aimed to cover the entire range of the species on the island. This, combined with limited available time in the field and the restricted accessibility to many parts of the range because of very steep and remote terrain, meant that we mostly collected data relatively close to roads. To maximize data collection in these circumstances, we planned the field data acquisition based on previous studies on the island, both by members of our team and through the expertise of the local administration (Cabildo Insular de La Palma).

2.2. Change Detection

Deciduous tree species have a distinct phenological cycle with synchronous leaf flush in spring and leaf shedding in autumn. In *C. sativa* on La Palma, this rhythm is presumably maintained and triggered by the photoperiod, even though harsh winter temperatures are missing, and the evolutionary driver of leaf shedding is no longer effective. In consequence, *C. sativa* can be mapped in a matrix of evergreen vegetation through digital change detection. Its most distinctive stage is its leaflessness between autumn and spring, making it a unique species in the otherwise evergreen ecosystem. To map *C. sativa*, we can therefore take advantage of the much larger change between seasons, in satellite images, in places where chestnut is (in-leaf vs. leafless) than in places where it is absent (in-leaf throughout)—making change detection through image regression appropriate for this purpose. We use image regression with the Landsat 8 images from 7 March and 29 July 2017, and with the Sentinel-2 images from 8 July 2018, and 13 February 2019 (Appendix A). By applying change detection to a pair of Landsat 8 images and to a pair of Sentinel-2 images, we can compare the detection performance of the two sensors.

Landsat 8 and Sentinel-2 surface reflectance data were obtained from USGS and Copernicus Open Access Hub. The Landsat 8 surface reflectance data are orthorectified data generated at 30 m grid cell resolution. The data are free from any atmospheric artefacts, illumination, and viewing geometry bias [45]. Similarly, the Sentinel-2 data are geometrically, radiometrically corrected, orthorectified, and spatially registered bottom-of-the-atmosphere reflectance products that are generated at 10, 20, and 60 m spatial resolutions [46]. Therefore, no further pre-processing of the images was carried out for those parameters. However, the part of the Landsat 8 image from March 2017 that contained clouds was cropped out with the help of Quality Assessment band shipped with the Landsat 8 surface reflectance product and compensated with an image from 3 February 2017 after histogram matching in R using the package RStoolbox [47]. A few cloud-contaminated pixels were left around the edges. The areas classified as agriculture and settlements by Corine land cover data 2018 were cropped out. Therefore, our study area, as calculated in R using the study area shapefile, covers approximately 545.82 km^2. The Sentinel-2 images used in this study are of 10 m spatial resolution.

Several techniques are used for digital change detection [39,48]; we chose image regression and differentiation for our analysis. Image regression does not need training data and can reduce atmospheric haze and sun angle effect [39]. Change detection, when used on its own, relies on thresholds to discern changed and unchanged pixels. Therefore, we integrated digital change detectionwith supervised classification, to avoid thresholds. The image regression technique assumes that the pixel values at time t1 are linear functions of the pixel values from time t2. Therefore, an image from one date can be regressed against the image from another date using least-squares regression [39,48].

Here, we used four different bands (blue [B], green [G], red [R], and near-infrared [NIR]) from each sensor, which we refer to as band 1, band 2, band 3, and band 4, respectively. Therefore, $t1_1^n$ is the image from the date 1 with n = 4 spectral bands, and $t2_1^n$ is the image from date 2 with the same number of spectral bands. We considered the image from one date to be a linear function of the image from the other date. Therefore, the image from date 1 was regressed on the image from date 2. We arbitrarily assigned the images from July as date 1.

$$t1_1^n = a + b\, t2_1^n + e \tag{1}$$

where a is intercept, b is slope, and e are the residuals.

If y_1^n is the predicted image on the image $t2_1^n$ from the regression line in the Equation (1), the changed image can be obtained by

$$d_1^n = y_1^n - t1_1^n \tag{2}$$

where d_1^n is the subtracted image from band 1 to n.

However, the change in pixels in the images obtained from the Equation (2) were not easily visible and discernible. The NIR band reflects more light from healthy vegetation than from stressed vegetation. Therefore, the NIR bands were subtracted from the red bands in the respective images obtained from the Equation (2).

$$D = d_3 - d_4 \tag{3}$$

where, D is the resulted change image.

Finally, the raster results were created using the band composition of D, d_3 and d_2, respectively, to obtain the changed pixels between two dates. Changed pixels gained from the image regression and image differentiation were compared with Google Earth images and field data.

2.3. Random Forest Classification

The supervised classification algorithm Random Forest (RF) was applied in this study to extract the *C. sativa* present spatial distribution. RF is a machine learning algorithm that works on bagging approaches: The algorithm grows multiple decision trees from the random subsets of data and gives a final decision based on the majority of votes from the resulting trees [40]. The algorithm has been reported to produce promising results [49].

The changed pixels may not all be associated with *C. sativa*. Therefore, *C. sativa*, forests and natural ecosystems were trained in QGIS based on the field reference data (Appendix B) and Google Earth images were taken as references. For the training data, the raster data obtained in Figures 2 and

3 were used to discern changed pixels (*C. sativa*), and unchanged pixels (forests and other natural ecosystems). The data were split into training and testing data in the ratio of 70% to 30% for each changed image from Landsat 8 and from Sentinel-2. The data used to train the model were cross-validated with ten-fold cross-validation. Supervised classifications were carried out in R with the caret [50] package on the images obtained from the image regression and image subtraction that include five bands as a stack. In the RF models, 650 trees were grown for each supervised classification—the out of bag error in the random forest classification reached a low level at 650 trees and was near-constant with more. The models were validated using the respective testing data (Appendix C).

2.4. Ecological Niche Modelling

Castanea sativa occurrence and coverage were recorded and mapped in the field from 11 April to 23 April 2019, mainly using road access. The sampling was conducted based on expert knowledge, and the change detection map (Figures 2 and 3) as well as through random *C. sativa* observations.The Global Positioning System (GPS) locations were recorded in the field for presence locations (Appendix B) using a WPL-2000 GPS device.

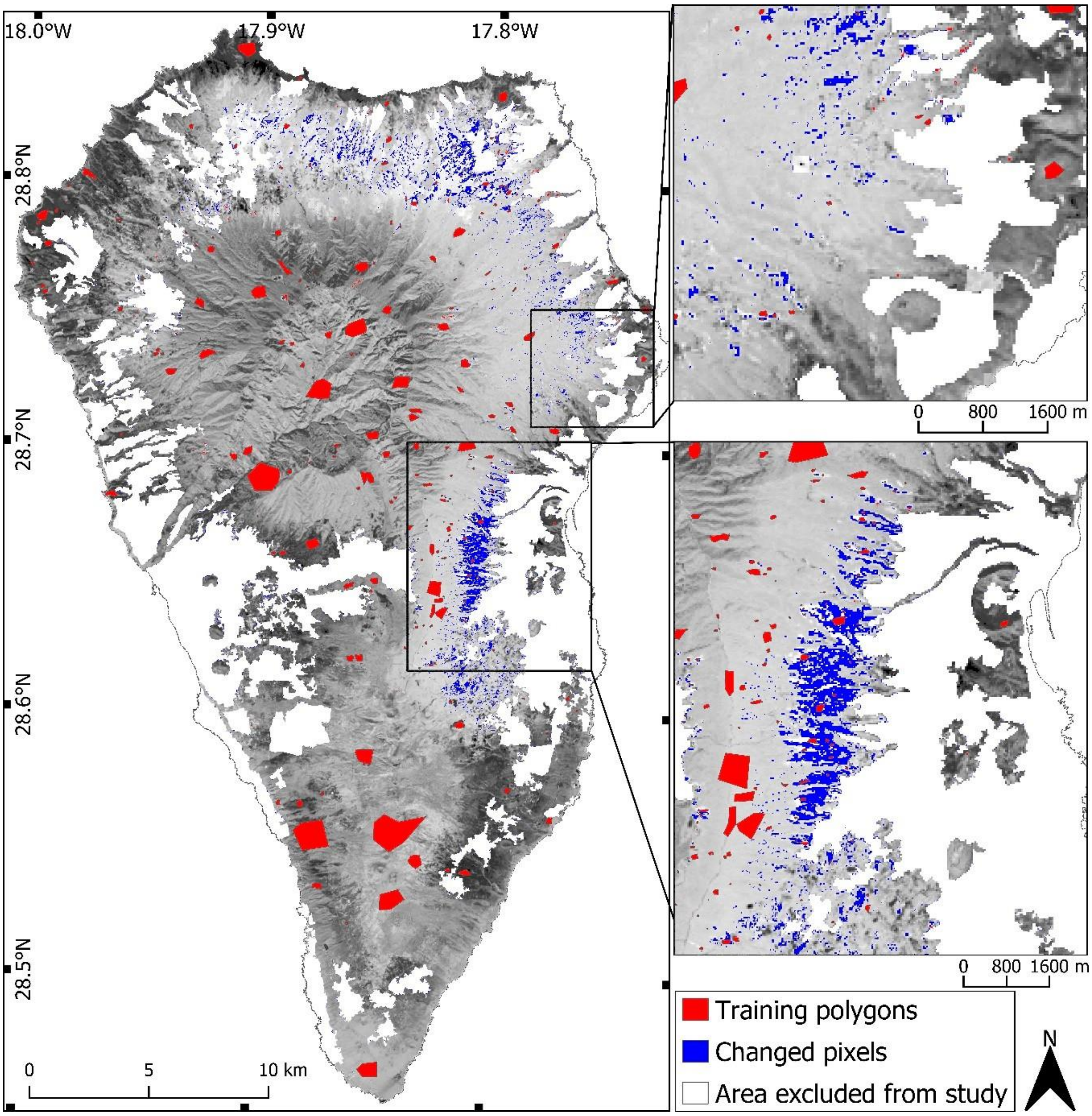

Figure 2. Changed pixels (proxy for leaf on/leaf off) between March 2017 and July 2017 in the Landsat 8 image obtained from the image regression and image differentiation, grayscale raster composite, red-NIR, red, green, each band with 1/3 saturation. Blue colour highlights changed pixels between those dates. Training polygons (red) are the training samples used to discriminate between changed and unchanged pixels. Settlements and other intensive human land-uses were cropped out (shown in white).

We retrieved a set of biotic and abiotic environmental variables from Cabildo Insular de La Palma, modified from [51]. Topographic information on aspect and slope was calculated in QGIS from the 2 m spatial resolution digital elevation model obtained from [52]. All environmental variables had a spatial resolution of 100 m except elevation, slope, and aspect; we aggregated the resolution of these to 100 m. After performing a correlation analysis on the entire set of environmental variables (r > 0.7, Appendix D), the following explanatory variables for ENMs remained: winter precipitation, summer precipitation, inter–annual precipitation, intra-annual precipitation, vegetation associations, solar radiation, elevation, slope, aspect, and parent materials (Appendix E). The mean annual temperature was highly correlated with elevation (r > 0.7), and mean annual precipitation was highly correlated with mean winter precipitation (r > 0.7) (Appendix D). We excluded mean annual temperature because La Palma possesses a high altitudinal gradient, and thus, the temperature difference is a major function of elevation even if aspect also plays a role due to differences in cloud cover and insolation. Similarly, mean annual precipitation was excluded because the precipitation exhibits a clear seasonal pattern with high amounts during winter and less precipitation in summer. From an ecological perspective, the variation in precipitation was a better choice to characterize habitat suitability of *C. sativa* compared to annual mean precipitation.

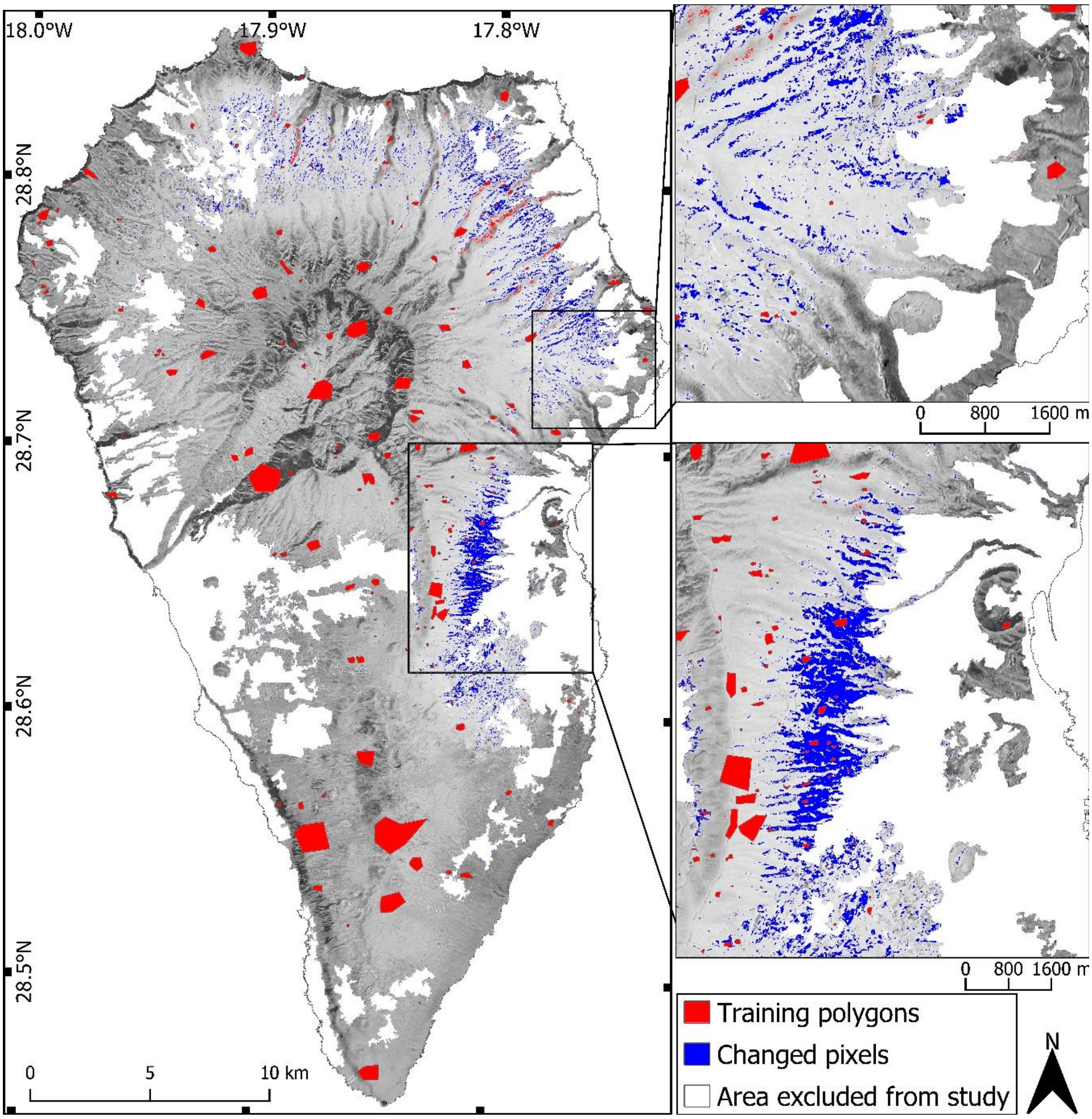

Figure 3. Changed pixels (proxy for leaf on/leaf off) between July 2018 and February 2019 in the Sentinel-2 image obtained from the image regression and image differentiation, grayscale raster composite, red-NIR, red, green, each band with 1/3 saturation. Blue colour highlights changed pixels between those dates. Training polygons (red) are the training samples used to discriminate between changed and unchanged pixels. Settlements and other intensive human land-uses were cropped out (shown in white, excluded from study).

For the ENMs, both species occurrence data from the field and from RS were used independently. We used R version 3.6.1 [53] and Quantum GIS (QGIS) version 3.6.3, as well as Google Earth applications. To obtain a habitat suitability map for *C. sativa*, we applied generalized additive models (GAMs), Maximum Entropy (MaxEnt) and Random Forest (RF), combining them into an ensemble model (EM) using biomod2 [54] (see results for each model algorithm in Appendix F). GAMs are data-driven, slightly modified regression models that use non-parametric, data-defined smoothers to fit nonlinear functions. GAMs are capable of modelling complex ecological response shapes [55,56]. MaxEnt is designed to estimate target probability distributions by finding the probability of maximum entropy [57]. The algorithm is extensively used in ENMs [58], but there are limitations when data are missing at the edges of species' distributions. In consequence, we opted for an EM, in order to obtain more robust outcomes than likely to be delivered by an individual modelling technique [59].

We randomly extracted 2500 RS species occurrence points from the area where spatial agreements in the resulting maps between both images were found. Data obtained were thinned with minimum spatial distances of 300 m and 100 m for RS data and field data, respectively, using spThin [60] package in R, to avoid spatial bias. We used 300 m for RS data thinning and 100 m for field data thinning because the RS data were uniformly rasterised, and field data were clumped due to inaccessible field sites. Applying 300 m in field data would result in far fewer species occurrences. The rationale for a 100 m minimum distance is that the environmental raster data that we used has a spatial resolution of 100 m. Hence, we wanted to avoid more than one species occurrence point in a single pixel. Final numbers of 241 and 172 occurrence points of RS and field, respectively, were used for modelling. With the biomod2 [54] package in R, the three different modelling approaches (GAMs, MaxEnt, and RF models) were integrated for the EMs. We generated the same number of pseudo-absence points as presence, taking prevalence into account [61,62] and excluding the area buffered by a 30 m radius from the species' occurrence points. The models were each run four times, with ten sets of pseudo-absence records that resulted in 120 models in total for each data set (field-collected species occurrence data and RS species occurrence data).

For EM projections, only models meeting the quality standards of total true skill statistic (TSS) > 0.7 and area under the receiver operating characteristic curve (AUC) > 0.8 were used. Individual models that did not meet these requirements were excluded from building the EM—including all the GAM and MaxEnt models [Appendix G]. Our resulting EMs were based on 50 and 34 single models for RS and field occurrence data, respectively. Mean of the weighted sum of probabilities, committee average across prediction, and mean probabilities across prediction of the ensemble forecasts were used to generate the suitable habitat map for *C. sativa*.

Receiver operating characteristic curve cut-offs that maximized the sum of specificity and sensitivity were used as the threshold to generate species habitat suitability (binary) maps. The binary maps were used to quantify the suitable habitat for *C. sativa* from each modelling approach and to analyse the variation in those areas with respect to the environmental variables used for the models.

3. Results

3.1. Change Detection

C. sativa occurrence locations detected by RS and in the field (Appendix B) had strong spatial agreements with the changed pixels (Figures 2 and 3), and model accuracy was high (Table 1). Additional pixels were also detected as changed pixels. However, they were ambiguous and were not distinguishable from other vegetation or attributes in the Google Earth reference image, and those locations were also not available from field data. Such ambiguities may have resulted from land-cover changes rather than from changes that occurred because of *C. sativa*'s phenological cycle.

Table 1: Statistical evaluation of Random Forest (RF) performance and map accuracy assessment. The overall accuracy and kappa were obtained from the testing data and the out-of-bag error (OOB) generated by RF of each of the model obtained from training data.

Sensors	**Parameters**		
	OOB Error %	**Overall Accuracy %**	**Kappa**
Landsat 8	1.29	98.8	0.798
Sentinel-2	0.44	99.5	0.878

The different sensors resulted in different areas of spatial coverage of *C. sativa* (Figure 4). The total coverages of *C. sativa* found in 2019 were 5.26 km2 in the Sentinel-2 and 6.72 km2 in the Landsat 8 images, which make 1% and 1.23%, respectively, of the total island area. Most of the detected occurrences of chestnut were from the eastern slopes and northern parts of the island. Only a few occurrences were detected on the southern slopes (Figure 4). Most of the occurrences were close to agricultural land and some were on lapilli fields. No *C. sativa* occurrences were detected in southern parts and coastal areas of the island. The *C. sativa* occurrence pixels in the Sentinel-2 are more scattered than in the Landsat 8 image (Figures 4 and 5). Even in the area where both sensors spatially agree, Landsat 8 was found to have a wider coverage than Sentinel-2 (Figure 5).

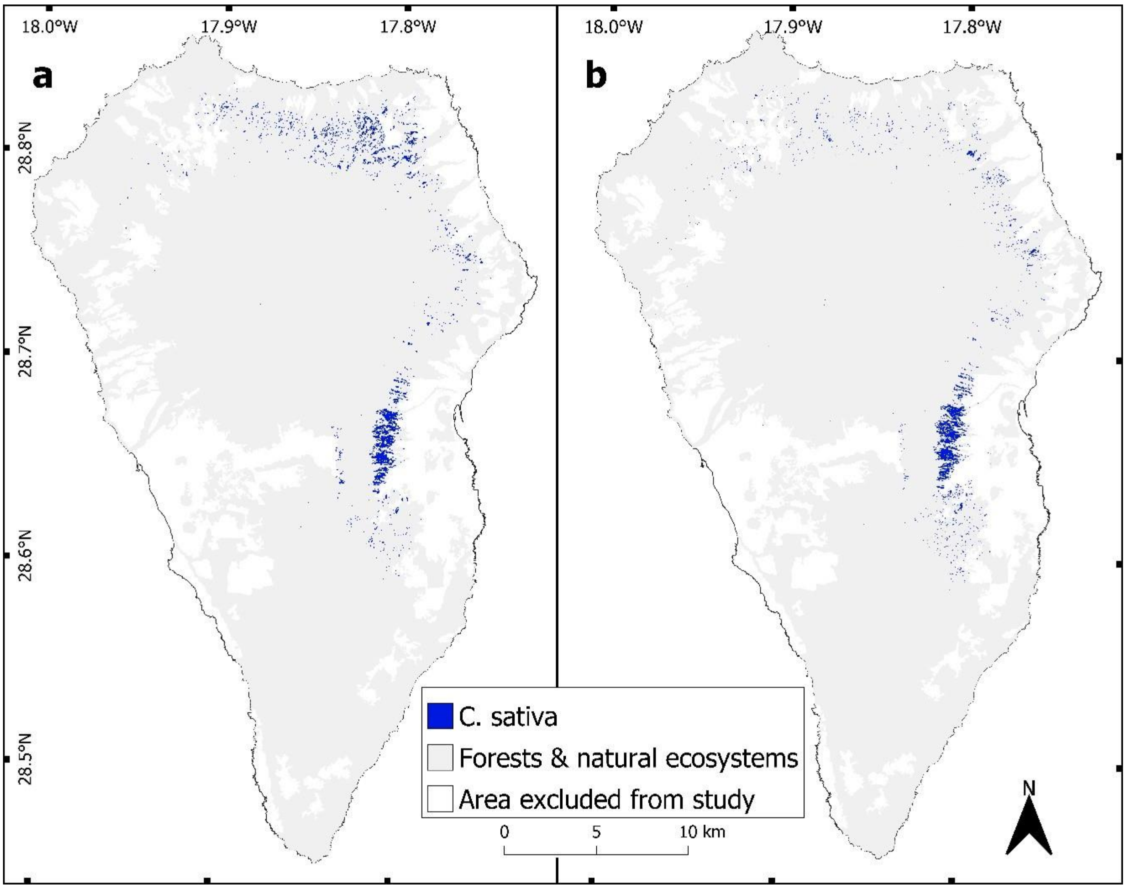

Figure 4. *C. sativa* spatial coverage (blue) detected on (**a**) the Landsat 8 image and (**b**) Sentinel-2 image obtained from the Random Forest (RF) classifications. The classifications were carried out

on the images obtained from the image regression and differentiation. 'Forests and natural ecosystems' (grey shading) are land cover not related to direct human land use. Settlement and agriculture (areas used for direct human purposes, including roads, buildings, agricultural lands, etc.) were cropped out and not included in the analysis.

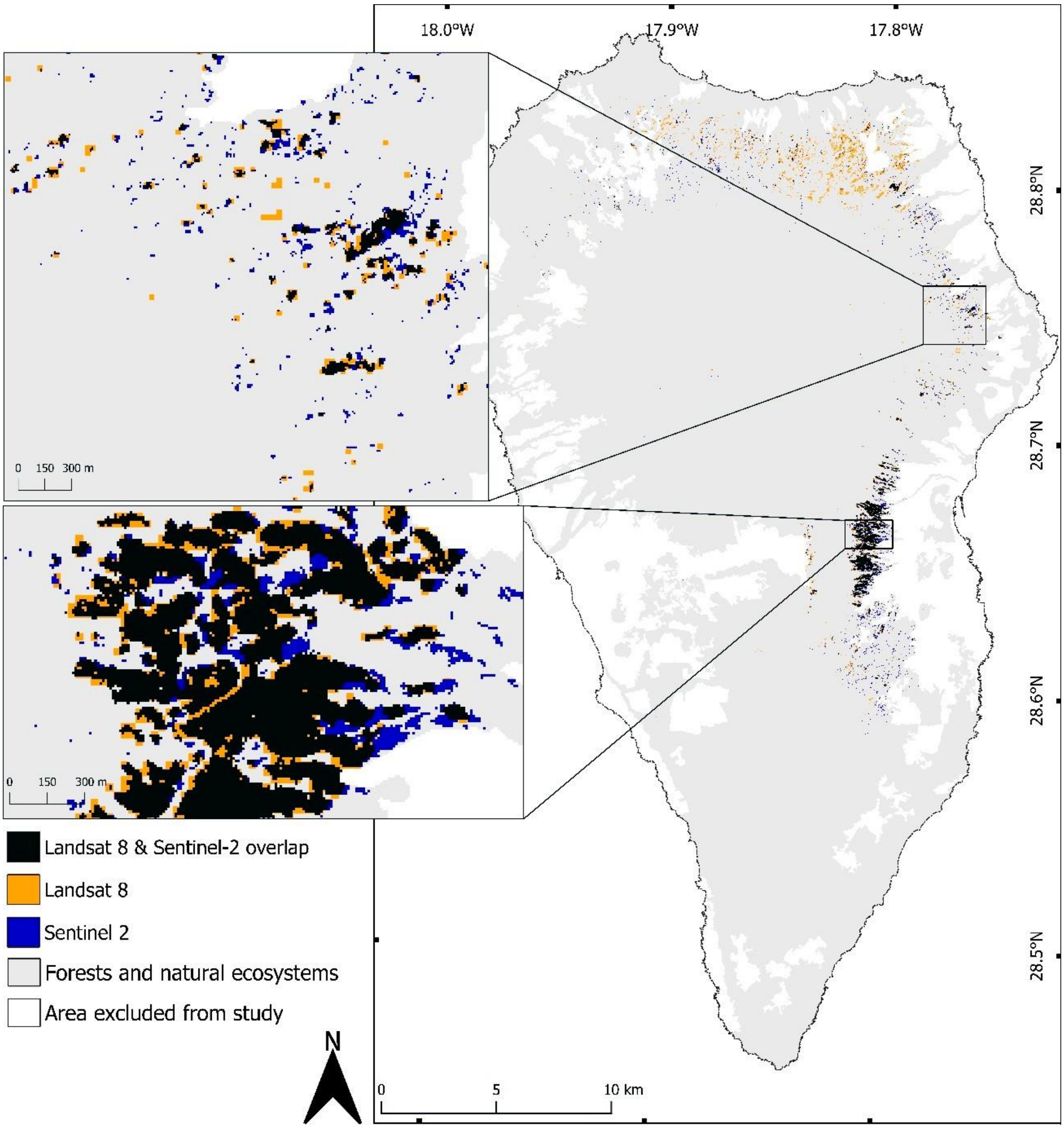

Figure 5. *C. sativa* spatial coverage in the images from the Landsat 8 and Sentinel-2 overlapping, Landsat 8 only, and Sentinel-2 only. Black are pixels where *C. sativa* was detected in both sensors' images; orange are pixels where *C. sativa* was only detected in the Landsat 8 image; blue are pixels where *C. sativa* was only detected in the Sentinel -2 image. The spatial resolution of Landsat 8 is 30 m, and Sentinel-2 is 10 m. 'Forests and natural ecosystems' (grey shading) are areas not directly used for human purposes. Human settlements, infrastructure, and agriculture (white) were cropped out.

Spatial coverage of *C. sativa* increases progressively from 400 m a.s.l. to 700 m a.s.l. and decreases above 700 m a.s.l. in the images from both the sensors (Figure 6).

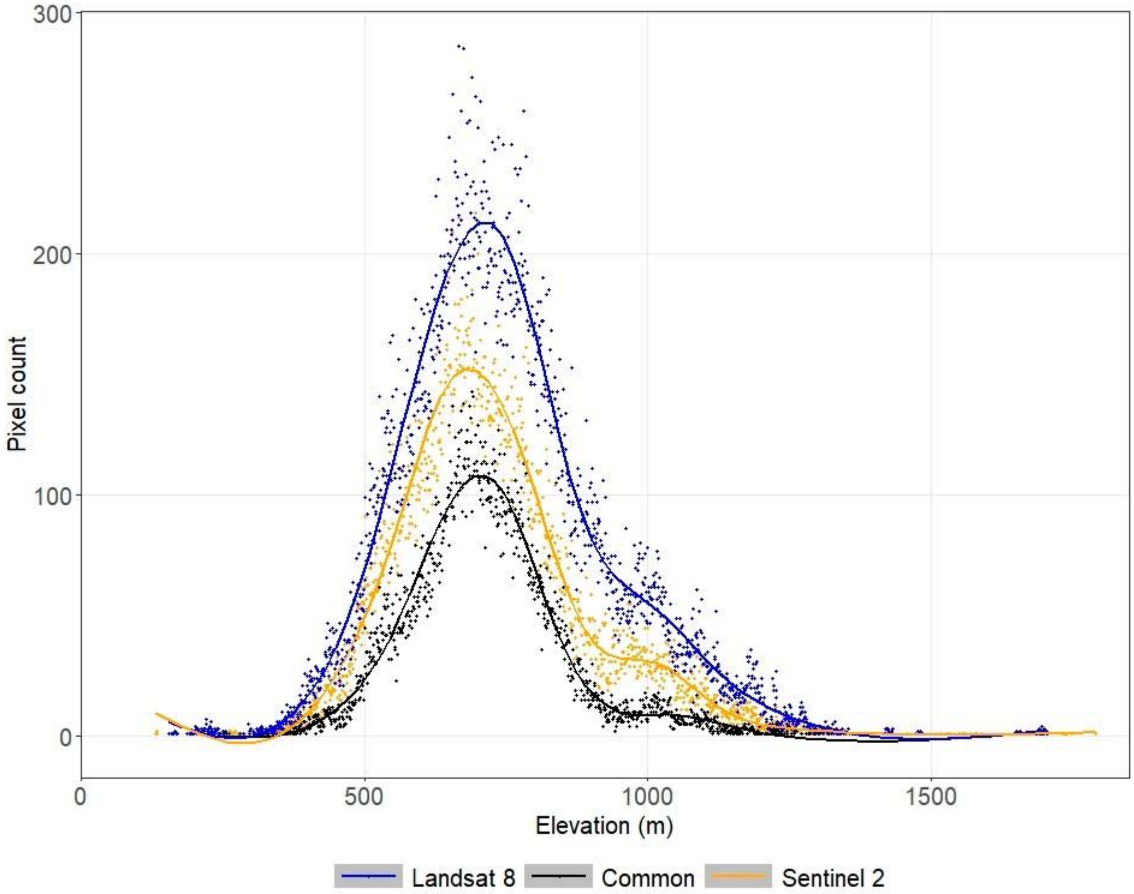

Figure 6. Number of pixels associated with *C. sativa* detected from RS along the altitudinal gradient. Values along the *y*-axis are the total number of pixels covered by *C. sativa* and values along the *x*-axis are the elevational gradient of La Palma (in m a.s.l.). Blue: Landsat 8 only; orange: Sentinel 2 only; black: shared pixels of both Landsat 8 and Sentinel-2. The spatial resolution of Landsat 8 was disaggregated to 10 m for comparison purpose.

3.2. Ecological Niche Modelling

All ENMs showed that habitats in the eastern and northern parts of the island—including the areas of present distribution—were more suitable for *C. sativa* (Figures 7 and 8, Appendices F and H for single model results). The ENMs based on species occurrences from field observation and the ENMs based on species occurrences from RS data were found to have very good AUC and TSS scores (Table 2 and Appendix I). The ENMs based on the RS data (Figures 7b and 8b) predicted larger suitable area for *C. sativa* compared to the prediction made by the models based on the field-collected species occurrence data (Figures 7a and 8a). However, the models based on the field-collected species occurrences seemed to cover more heterogeneous areas, even though the total suitable area for the species was predicted to be less in the field-collected species occurrence-based models.

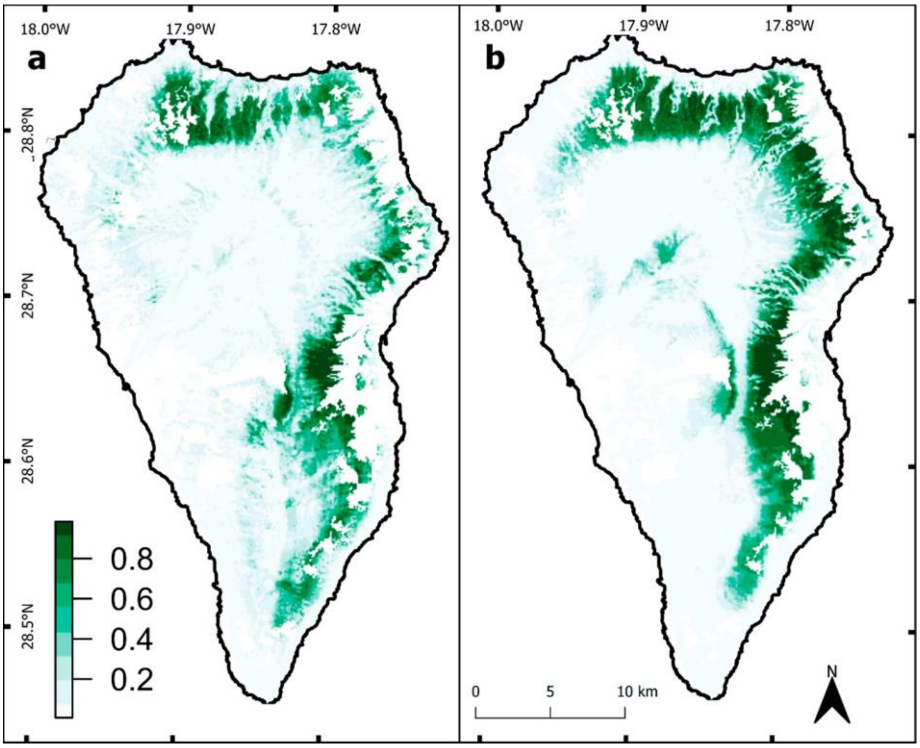

Figure 7. *C. sativa* habitat suitability maps obtained from the ecological niche modelling (ENM) using ensemble models (EM). (**a**) The map obtained from the model based on field-collected species occurrence data. (**b**) The map obtained from the model based on the species occurrence data derived from remote sensing. The vertical legend on the bottom-left shows the degree of suitability; values closer to 1 indicate comparatively higher habitat suitability.

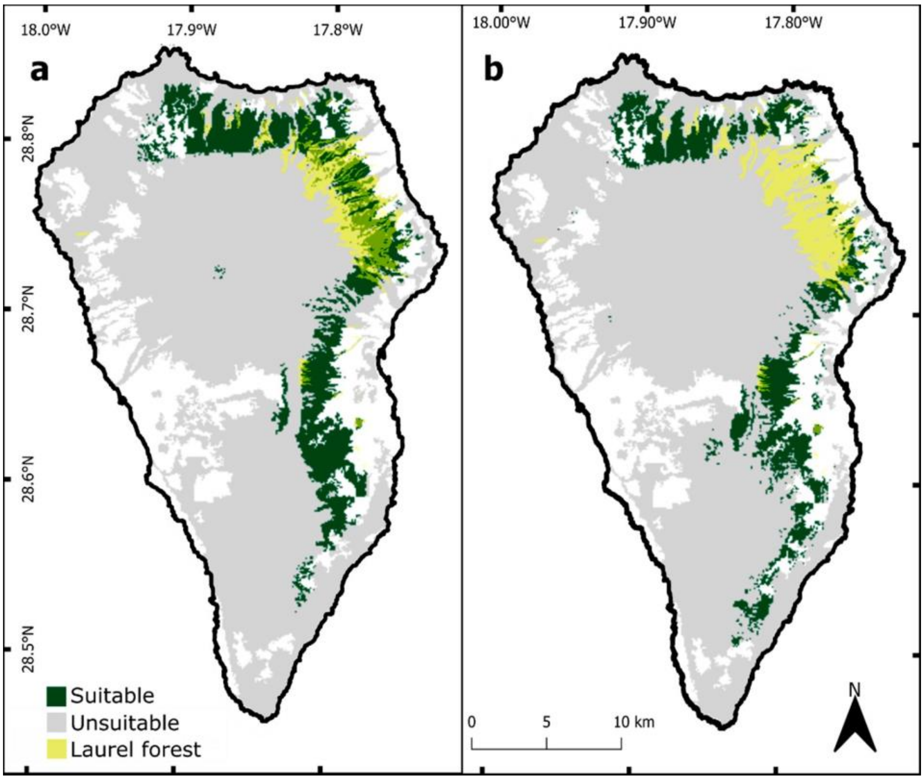

Figure 8. *C. sativa* binary habitat suitability maps from (**a**) the ensemble model (EM) based on the field-collected species occurrence locations, and from (**b**) the EM based on RS-derived species occurrence locations. These maps are the outcomes of the binary transformation of the predicted maps from the respective models. The extent of the laurel forest (based on the plant communities defined by Del Arco Aguilar et al. [63]) is indicated as a yellow semi-transparent layer.

Table 2. Statistical parameters of model performances, thresholds applied to convert maps resulted from each modelling approach to binary maps and area suitable for *C. sativa*. All the parameters are means of ensemble model outputs

Model	Parameters							
	AUC		Threshold		TSS		Area (km^2)	
	Field	RS	Field	RS	Field	RS	Field	RS
EM	0.982	0.961	564.83	634.42	0.885	0.805	66.73	90.12

4. Discussion

This study assesses the current and potential distribution of non-native C. *sativa*, invading the endemic species-rich ecosystems of La Palma. The establishment of deciduous chestnut (*C. sativa*) on La Palma and its spread into the native laurel forest has the potential to initiate a secondary succession that may change the evergreen broadleaved forest towards a different ecosystem in terms of phenology and light regime. *C. sativa* was introduced on the island approximately 500 years ago for agricultural purposes [21]. Extremely steep and unstable slopes restrict access to the sites. Further, only estimating the current distribution of the alien species would be problematic because the current situation is just a snapshot of the potential occupied space and ecological niche on the island [64]. Therefore, it is important to combine in-situ and RS data with modelling approaches.

We found through this combined methodology that deciduous chestnut trees and forest today occupy approximately 1.2% of the total area of natural ecosystems (i.e., non-agricultural and excluding infrastructure and settlements) on La Palma, with a further 12–17% representing suitable habitat that is not yet occupied by this species. This is important because this non-native deciduous tree species can reach high canopy cover and has the potential to strongly modify the species composition of the original evergreen forest ecosystems, as well as the nature of the ecosystem (e.g., leafless in winter) and the services it provides. Comparing the current spatial distribution of *C. sativa* in La Palma obtained from RS and the results obtained from ENMs, we can see that *C. sativa* has not yet reached its full potential distribution on La Palma. Our results show varying areas of available suitable habitats for *C. sativa* that could be occupied in the future, depending on the reference data and modelling algorithm. However, in all cases, there is a considerable overlap of the species' niche with the distribution of the native laurel forest ecosystem in the eastern and northern slopes of the island.

Despite their southern location, the Canary Islands are clearly part of the Holarctic realm. Most of the plant families native to the islands are very abundant across the Mediterranean. In addition, the ecosystems of the archipelago are strongly linked to Mediterranean climate and ecosystems through their evolutionary history and phylogenetic relations. Although the Macaronesian islands have many endemic species, the perennial and woody taxa that shape the islands' forest and shrubland ecosystems are either shared with the Mediterranean region of Europe (native non-endemics on the Canaries) or in the case of endemic species have their closest relatives there, and not in the Palaeotropcis (e.g., *Laurus*, *Viburnum*, *Prunus*, *Pistacia*, *Olea*, *Arbutus*, *Asparagus*, *Cistus*, *Echium*, *Carlina*, *Genista*, *Helianthemum*, *Hypericum*, *Lavandula*, *Micromeria*, *Ononis*, *Rhamnus*, *Rubia*, *Ruscus*, *Salvia*, *Sideritis*, *Smilax*, *Sonchus*, *Thesium*). Several native ferns of the laurel forest are also abundant in moist forests of the Mediterranean (e.g., *Asplenium hemionitis*, *Selaginella denticulata*, *Adiantum capillus-veneris*, *Polystichum setiferum*, *Woodwardia radicans*). Sub-Mediterranean species such as *C. sativa* find adequate climatic conditions mainly at mid-elevation of the volcanic mountains on those islands that exhibit a pronounced topography.

Habitat suitability is calculated by models that are based either on in situ data or on RS data. Our study combines a slightly modified change detection technique with machine learning supervised classification algorithms. The change detection technique is especially suitable for invasive plant species detection if the species exhibits clear phenological changes compared to native vegetation through time, as shown by the detection of glossy buckthorn (*Frangula alnus* Mill.) spreading into forests of southern Quebec, Canada, by applying a linear temporal unmixing model to a time series of the normalized difference vegetation index (NDVI) derived from Landsat 8 Operational Land Imager (OLI) [65]. The RS-based *C. sativa* spatial distribution assessments yielded differences in spatial coverage, with the area estimated by Landsat 8 slightly higher than that estimated by Sentinel-2. The variation in the image resolutions between two sensors may be one of the reasons for greater spatial coverage estimated from the Landsat imagery. As Landsat 8 images have a spatial resolution of 30 m and Sentinel-2 images (used in this study) have a spatial resolution of 10 m, one pixel of Landsat 8 is equivalent to 9 pixels of Sentinel-2.

Smaller spatial extent of *C. sativa* area extracted from Sentinel-2 compared to Landsat 8 translated into less modelled spatial coverage based on Sentinel-2 compared to Landsat 8. Both sensitivity and grain size in spatial resolution can lead to such findings. Image quality, especially in a heterogeneous environment where plant species cannot easily be discerned, may result in spectral mixing [66], which is poorly represented by a low-spatial-resolution image. Thus, with lower spatial resolution, classification accuracy tends to decrease [67]. However, this relationship can reverse when using very high spatial resolution imagery [68]. Furthermore, residual yet marginal cloud coverage on the image from 7 March 2017, could have influenced the performance of the Landsat 8 scene.

The survival of *C. sativa* across the heterogeneous environment in La Palma suggests that the species shows high adaptive ability. We find that the moist and humid regions with broad-leaved trees, shrubs, and herbs are most suitable for the species. Similarly, Ríos-Mesa et al. [21] stated that on Tenerife, *C. sativa* is more dominant in the regions where trade winds humidify the area.

Ecological theory suggests that species-rich ecosystems can be more resistant to invasion [69–71]. Since many niches are not occupied on islands, it is expected that more species will naturalize in the future [72]. Such an increasing saturation of species richness could enhance the functioning of ecosystems [73]. However, individual alien species may also modify important ecosystem functions, causing negative effects even centuries after their establishment when replacing other key species such as dominant plant functional types [13].

The replacement of one dominating plant functional type by another can particularly affect sensitive ecosystems on very steep slopes in a humid zone. The natural stability of the laurel forest on these slopes is astounding and results from its species diversity and the clonal root systems of the contributing tree species in combination with their evergreen foliage [44]. A regime shift away from long-lived, clonal evergreen trees can create new risks for the human population downslope through altered run-off, erosion and landslide potential. The respective loss of diversity caused by an invading species also affects ecosystem stability [70].

The development of a forest with deciduous canopy in contrast to the native evergreen forest is creating a novel ecosystem in the Canary Islands, where such ecosystems did not exist before. The emergence of novel ecosystems with altered species composition, structure, and functioning [74] is a common phenomenon worldwide. Such substantial changes are in the first instance linked with uncertainty because expert knowledge on such novel systems does not exist. The lost system may also matter. Functional traits, structures, phenology, and biodiversity can be assessed for newly emerging ecosystems and compared to the replaced ones. In the case of the alien deciduous chestnut forest on the Canary Islands, a highly diverse and evergreen forest is replaced by monodominant stands with seasonal foliage. Consequences for species loss, erosion control, landslide threat, and carbon sequestration are to be expected and require further monitoring [13].

Here we used open-access RS data, which come at the expense of relatively coarse spatial and spectral resolutions. We could, nevertheless, achieve a very high detection accuracy because the application of multi-date RS data made it possible to effectively resolve the phenological differences of deciduous *C. sativa* in this particular study system. When such clear spectral differences are known, expensive very-high-resolution RS data are not required to detect invasive species, even though most studies recommend such RS data for high accuracy. For example, multispectral Quickbird data including 4 bands and a spatial resolution of 2.4 m were used to map invasive *Tamarix* species along the Colorado River [75]. However, commission errors were still high due to the relatively coarse spectral resolution. Another comparison revealed that AISA hyperspectral imagery is more effective than Quickbird in identifying invasive individuals [76]. Müllerová et al. [77] investigated the effectiveness of panchromatic, multispectral, and colour very high spatial resolution aerial photography (resolution 0.5 m) and medium spatial resolution satellite data (Rapid Eye, resolution 5 m) in monitoring the noxious invasive giant hogweed (*Heracleum mantegazzianum* Sommer & Levier) using pixel- and object-based image analysis. The authors found that object-based analysis of aerial 0.5 m resolution data during the flowering period resulted in high detection accuracy, while pixel-based analysis of 5 m resolution satellite data achieved moderate accuracy. Underwood et al. [78] detected iceplant (*Carpobrotus edulis* L.) and jubata grass (*Cortaderia jubata* Lemoine ex Carriere) in Mediterranean-type ecosystems of California using Airborne Visible and Infrared Imaging Spectrometer (AVIRIS) imagery with 4 m resolution. These RS data were particularly useful because both invasive species could be distinguished from co-occurring species by leaf water content. Downy brome (*Bromus tectorum* L.) was mapped in semi-arid rangeland ecosystems of Washington state, USA, using AVIRIS imagery with 4 m [79]. The authors compared the detection accuracy from single-date and multi-date AVIRIS data applying a filtering algorithm for image classification. The accuracy was higher for multitemporal RS data that could resolve phenological differences through time. In terms of the effectiveness of multitemporal RS data, Hestir et al. [80] and Evangelista et al. [31] show that omission errors for mapping phenologically different and invasive plant species depend strongly on acquisition dates of RS images. Interestingly, in the Great Basin, *B. tectorum* could only be detected with very low accuracy (35%) using multitemporal data from Landsat MSS, TM, and ETM+, which are spaceborne sensors with relatively low spectral and spatial resolution [81]. However, the invasive shrubs *Frangula alnus* Mill. and *Rhamnus cathartica* L. were sufficiently mapped in Ohio and Michigan States, USA, by applying multitemporal Landsat TM and ETM+ satellite images [82]. In addition, airborne LiDAR and hyperspectral sensors are commonly used in precision agriculture and forestry to map crop quality, weeds, and pests [83], and thermal spectrometers have also proven to be very advantageous for detecting invasive plant species [84]. In view of all these examples, it remains challenging to select the appropriate RS data, particularly concerning the temporal, spatial and spectral resolution, to efficiently detect invasive plant species among native vegetation [30]. However, given the inaccessibility and high costs of very-high-resolution RS data, free and open-access RS data should be promoted in research and conservation when they are appropriate. Here we prove the effectiveness of open-access RS data for invasion science and management despite relatively coarse spatial, temporal, and spectral resolution of RS data.

Ensemble models perform better than single models in predicting invasive plant species' habitat suitability [85]. Nevertheless, using correlative models such as ENMs to predict the potential distribution of invasive species can be problematic because invasive species can establish in environmental niches that are new or very restricted compared to their native range [86]. Moreover, our models do not address the question of community saturation, i.e., to what degree environmental drivers limit species richness, composition and invasion of communities [73]. Moreover, the choice of environmental predictors drives the explanation of distributions [30]. The prediction success additionally depends on the frequency of test occurrences that makes prediction success a potentially biased estimator of model performance [61]. Hence, invasives' distributions in non-native ranges may be severely under- or overestimated by ENMs. However, such predictions are often the only reasonable way to guide conservationists to potential areas of invasion [87,88]. Range expansions of invasive species can happen rapidly due to changes in the species' invasibility or environmental factors such as land use and climate change [89]. Consequently, models based on species occurrence points should be interpreted as risk of species establishment, not species abundance, or impact [90].

Correlative model predictions involving abiotic factors only are also criticized because real invasion processes such as interspecific competition are ignored [91]. Mechanistic or process-based models may thus perform better than correlative models. However, process-based models require greater understanding of the invasion process than is usually available. Notably, biological mechanisms can be revealed by RS approaches. Asner et al. [33] revealed climate interactions promoting the invasive evergreen tree *M. faya* spreading into Hawaiian rainforest by analysing a time series of EO-1 Hyperion satellite data only. Once mechanistic models are applied, their performance can be validated by species distribution data directly derived from RS [30].

Detection accuracy depends not only on RS data and modelling approaches but also on algorithms applied for image classification. In Mediterranean forests, spaceborne QuickBird and airborne ADS40-SH52 imagery was combined to identify individual trees of the Iberian wild pear (*Pyrus bourgaeana* Decne.) [67]. Applying maximum likelihood approach and support vector machines on a pixel-by-pixel basis yielded different results depending on the combination of RS data and classification algorithms. Müllerová et al. [77] conclude that object-based analysis of aerial photography with 0.5 m resolution taken during the flowering period resulted in high detection accuracy, while pixel-based analysis of 5 m resolution Rapid Eye data achieved moderate accuracy in monitoring the noxious invasive giant hogweed (*H. mantegazzianum*).

The spectral signatures of species change through time due to biochemical, physiological, phenological, and environmental factors [92]. This variation of spectra limits the transferability of the relationships between spectral signatures, species, and environments to other study systems. Consequently, we recommend adapting our methodological approach individually to other systems.

5. Conclusion

This study identifies the probability of invasion of the introduced *C. sativa*, with particular focus on the laurel forest ecosystems of the island of La Palma, Canary Islands, Spain. Even if the spread of this deciduous tree species has been slow until now, major uncertainties arise from the fact that represents a plant functional type different from the zonal vegetation. Only two, rare native deciduous tree species can be found naturally (*Salix pedicellata* subsp. *canariensis* (C. Sm. ex Link) A. K. Skvortsov; *Sambucus palmensis* Link), along semi-permanent brooks and streams. However, these native deciduous species play no role in the natural evergreen forest ecosystems of the island.

The projected potential for the replacement of an evergreen broadleaved laurel forest rich in endemic tree species by a deciduous broadleaved forest formed by one introduced tree species does not inform about the speed of such processes. Inertia in long-lived tree species that can sprout from their rootstock is likely to avoid a rapid transition. However, a very resilient and stable ecosystem could be replaced by a less resilient and less stable one with only seasonal leaf cover and low species diversity. The steep and moist slopes of the island limit the accessibility in the field. We therefore recommend monitoring the future spread of *C. sativa* using RS approaches, as herein.

Our findings can be applied to other islands of the archipelago, where comparable climatic conditions are found and the characteristic laurel forest occurs, i.e., El Hierro, La Gomera, Tenerife, and

Gran Canaria. For these islands, our findings provide an early warning to generate awareness of possible invasion processes and to start proactive measures to avoid invasion into unique, valuable, and remnant laurel forests. Our results can also be transferred to the islands of Madeira and the Azores, where climatic conditions are very likely even more appropriate for *C. sativa*. In the case of the Azores, the laurel forest is almost completely replaced by conifer plantations and other invasive species (e.g., *Pittosporum undulatum* Vent., *Hedychium gardnerianum* Sheppard ex Ker Gawl.) This makes the preservation of the Canary Island laurel forest an even more important priority in the international context.

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Appendix A

Table A1: Satellite images used in the study.

Sensor	**Scene ID**
Landsat 8	LC082080402017072901T1-SC20190612132658
Landsat 8	LC082080402017030701T1-SC20190128221754
Landsat 8	LC082080402017020301T1-SC20190612132509
Sentinel-2	S2A_MSIL2A_20180708T120331_N0208_R023_T28RBS_20180708T141805
Sentinel-2	2A_MSIL2A_20190213T120321_N0211_R023_T28RBS_20190213T172742

Appendix B

Table A2: Total number of training and testing data used in Random Forest classification.

Sensor	**Data**	
	Training	Testing
Sentinel-2	101501	43499
Landsat 8	11557	4952

Appendix C

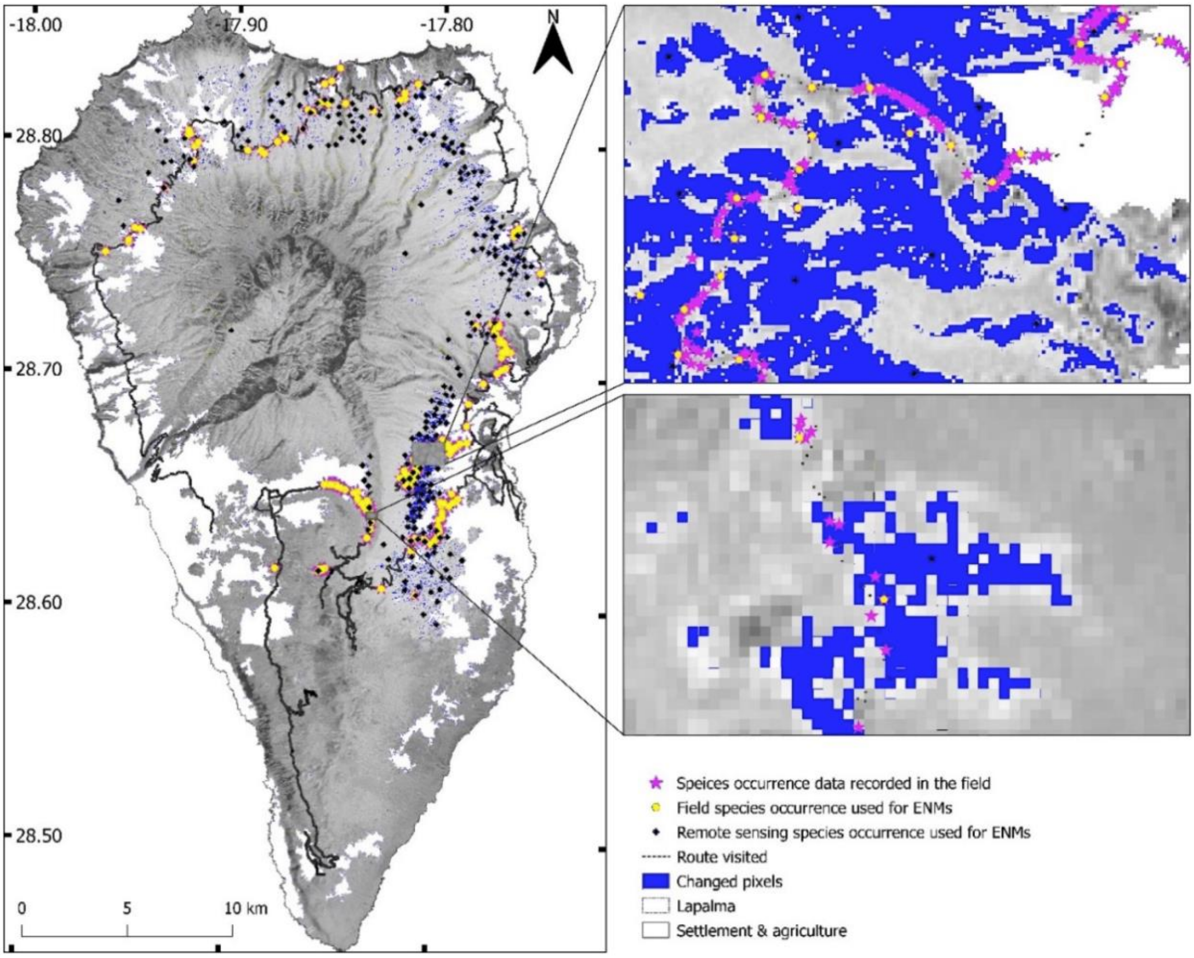
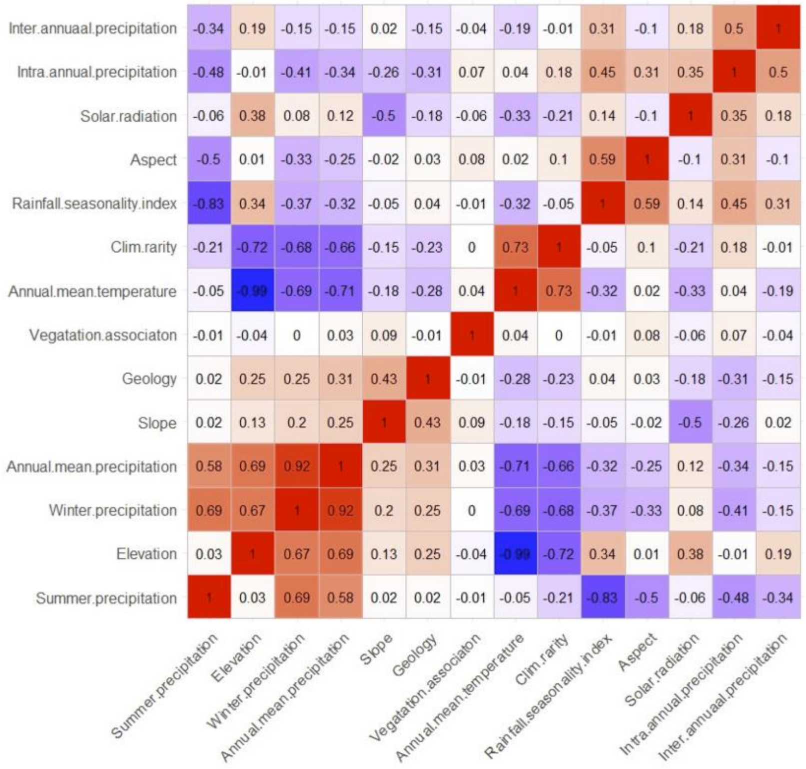


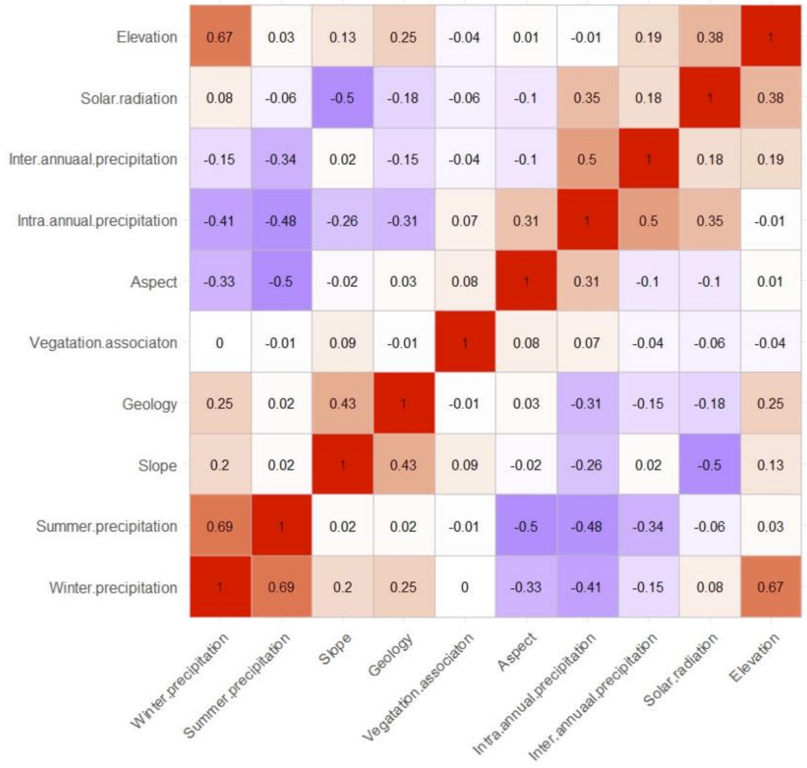
Figure A1: Species occurrence locations recorded from field and species occurrence locations used in Ecological niche modellings (ENMs) with two cut-out sections for details.

Appendix D



	Summer.precipitation	Elevation	Winter.precipitation	Annual.mean.precipitation	Slope	Geology	Vegatation.associaton	Annual.mean.temperature	Clim.rarity	Rainfall.seasonality.index	Aspect	Solar.radiation	Intra.annual.precipitation	Inter.annuaal.precipitation
Inter.annuaal.precipitation	-0.34	0.19	-0.15	-0.15	0.02	-0.15	-0.04	-0.19	-0.01	0.31	-0.1	0.18	0.5	1
Intra.annual.precipitation	-0.48	-0.01	-0.41	-0.34	-0.26	-0.31	0.07	0.04	0.18	0.45	0.31	0.35	1	0.5
Solar.radiation	-0.06	0.38	0.08	0.12	-0.5	-0.18	-0.06	-0.33	-0.21	0.14	-0.1	1	0.35	0.18
Aspect	-0.5	0.01	-0.33	-0.25	-0.02	0.03	0.08	0.02	0.1	0.59	1	-0.1	0.31	-0.1
Rainfall.seasonality.index	-0.83	0.34	-0.37	-0.32	-0.05	0.04	-0.01	-0.32	-0.05	1	0.59	0.14	0.45	0.31
Clim.rarity	-0.21	-0.72	-0.68	-0.66	-0.15	-0.23	0	0.73	1	-0.05	0.1	-0.21	0.18	-0.01
Annual.mean.temperature	-0.05	-0.99	-0.69	-0.71	-0.18	-0.28	0.04	1	0.73	-0.32	0.02	-0.33	0.04	-0.19
Vegatation.associaton	-0.01	-0.04	0	0.03	0.09	-0.01	1	0.04	0	-0.01	0.08	-0.06	0.07	-0.04
Geology	0.02	0.25	0.25	0.31	0.43	1	-0.01	-0.28	-0.23	0.04	0.03	-0.18	-0.31	-0.15
Slope	0.02	0.13	0.2	0.25	1	0.43	0.09	-0.18	-0.15	-0.05	-0.02	-0.5	-0.26	0.02
Annual.mean.precipitation	0.58	0.69	0.92	1	0.25	0.31	0.03	-0.71	-0.66	-0.32	-0.25	0.12	-0.34	-0.15
Winter.precipitation	0.69	0.67	1	0.92	0.2	0.25	0	-0.69	-0.68	-0.37	-0.33	0.08	-0.41	-0.15
Elevation	0.03	1	0.67	0.69	0.13	0.25	-0.04	-0.99	-0.72	0.34	0.01	0.38	-0.01	0.19
Summer.precipitation	1	0.03	0.69	0.58	0.02	0.02	-0.01	-0.05	-0.21	-0.83	-0.5	-0.06	-0.48	-0.34

Figure A2: Pearson correlation coefficients of environmental raster used in ecological niche modelling (ENM).



	Winter.precipitation	Summer.precipitation	Slope	Geology	Vegatation.associaton	Aspect	Intra.annual.precipitation	Inter.annuaal.precipitation	Solar.radiation	Elevation
Elevation	0.67	0.03	0.13	0.25	-0.04	0.01	-0.01	0.19	0.38	1
Solar.radiation	0.08	-0.06	-0.5	-0.18	-0.06	-0.1	0.35	0.18	1	0.38
Inter.annuaal.precipitation	-0.15	-0.34	0.02	-0.15	-0.04	-0.1	0.5	1	0.18	0.19
Intra.annual.precipitation	-0.41	-0.48	-0.26	-0.31	0.07	0.31	1	0.5	0.35	-0.01
Aspect	-0.33	-0.5	-0.02	0.03	0.08	1	0.31	-0.1	-0.1	0.01
Vegatation.associaton	0	-0.01	0.09	-0.01	1	0.08	0.07	-0.04	-0.06	-0.04
Geology	0.25	0.02	0.43	1	-0.01	0.03	-0.31	-0.15	-0.18	0.25
Slope	0.2	0.02	1	0.43	0.09	-0.02	-0.26	0.02	-0.5	0.13
Summer.precipitation	0.69	1	0.02	0.02	-0.01	-0.5	-0.48	-0.34	-0.06	0.03
Winter.precipitation	1	0.69	0.2	0.25	0	-0.33	-0.41	-0.15	0.08	0.67

Figure A3: Pearson correlation coefficients of environmental raster used in ecological niche modelling (ENM).

Appendix E

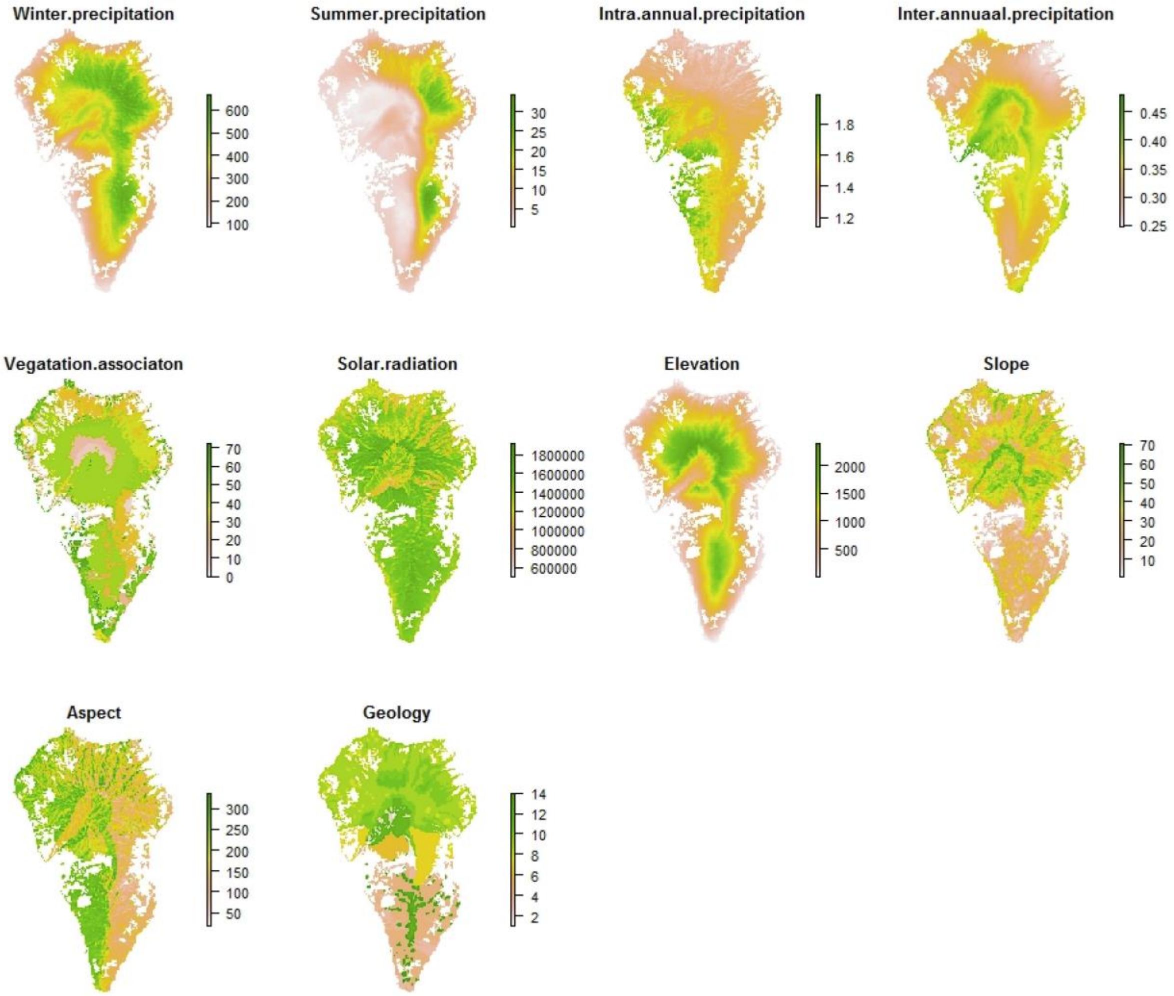


Figure A4: Environmental raster used in ecological niche modelling (ENM); Data surfaces are modified from data published in Irl et al., 2015.

Appendix F

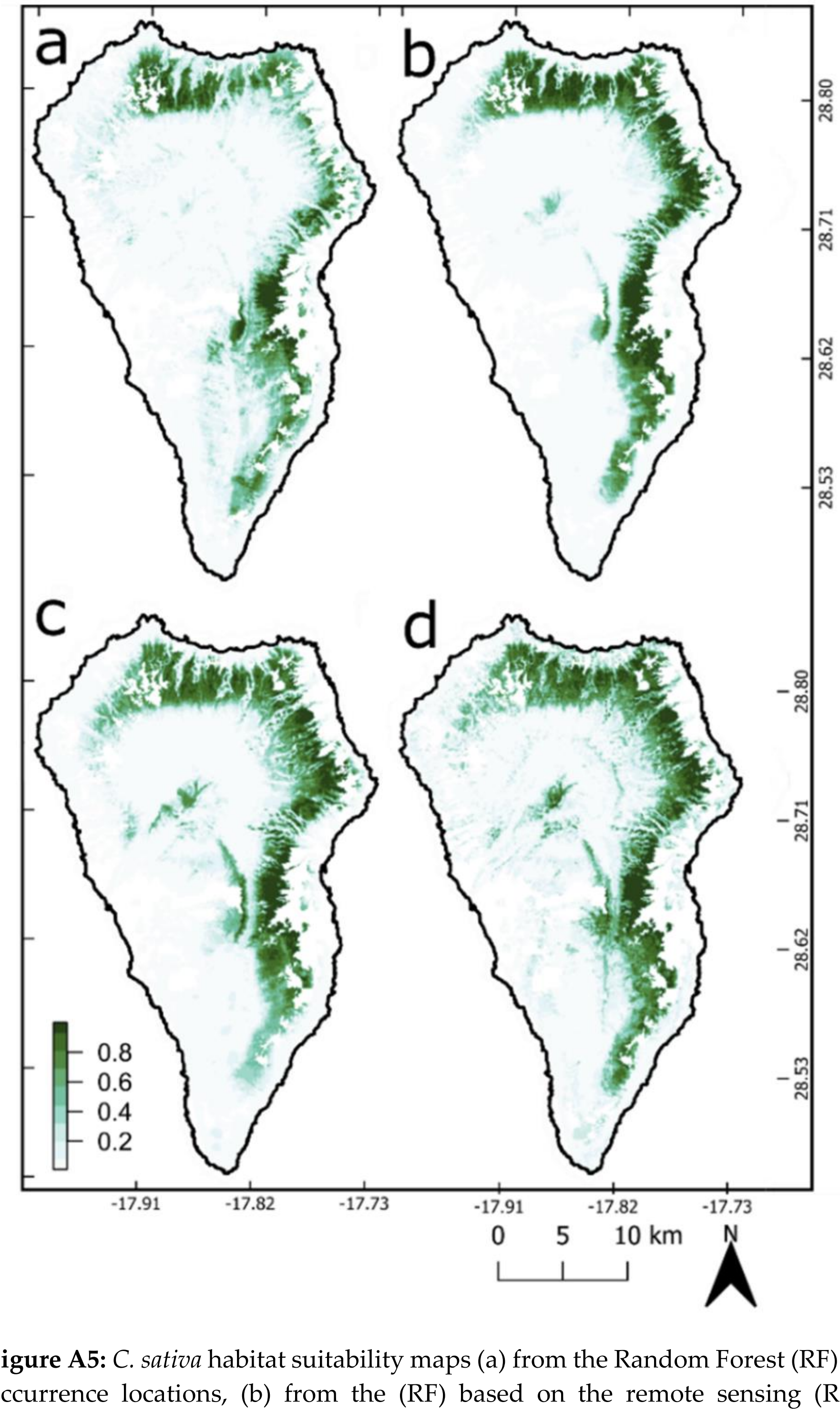


Figure A5: *C. sativa* habitat suitability maps (a) from the Random Forest (RF) field-collected species occurrence locations, (b) from the (RF) based on the remote sensing (RS) species occurrence locations, (c) from the Generalized Additive Linear Model (GAM) based on the RS species occurrence locations and (d) from the Maximum Entropy (MaxEnt) Model based on the RS species occurrence locations.

Appendix G

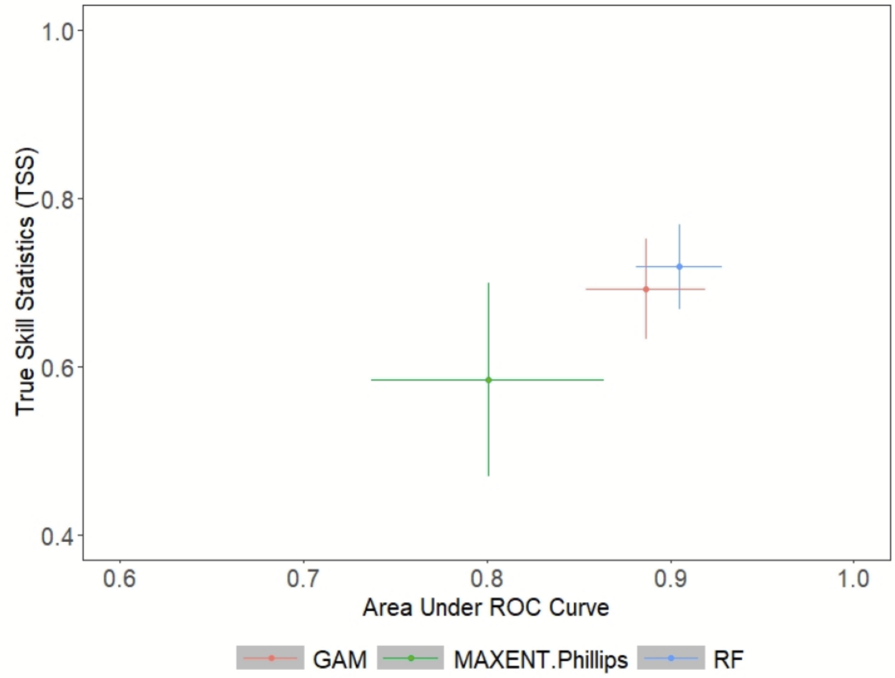


Figure A6: The initial model evaluation for the models from the RS data. Among the 120 models, the models which have True Skill Statistics and Area Under ROC scores greater than 0.7 and 0.8 respectively were only considered in habitat suitability modelling.

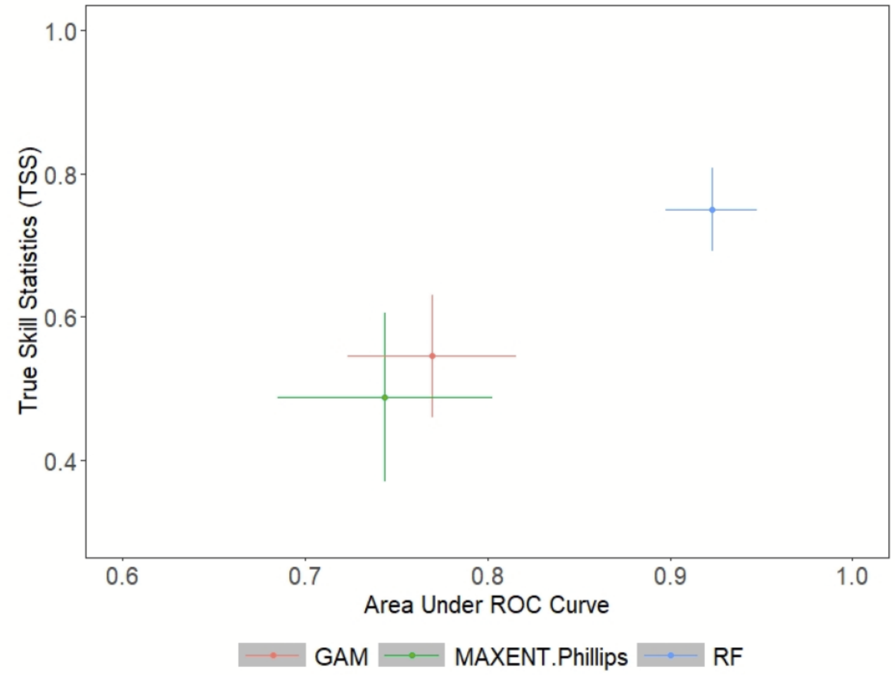


Figure A7: The initial model evaluation for the models from the Field data. Among the 120 models, the models which have True Skill Statistics and Area Under ROC scores greater than 0.7 and 0.8 respectively were only considered in habitat suitability modelling.

Appendix H

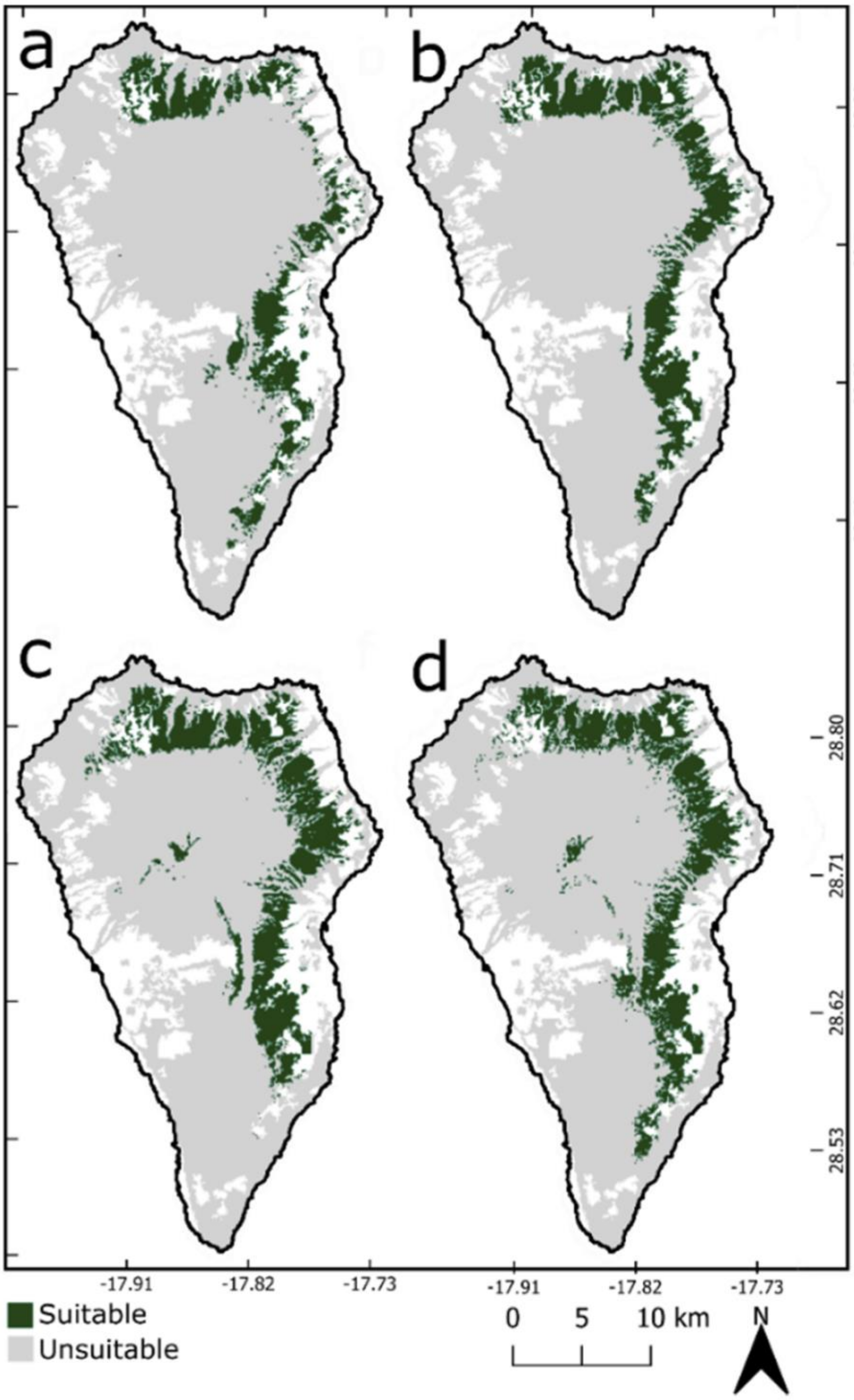


Figure A8: *C. sativa* presence absence maps (a) from the Random Forest (RF) field-collected species occurrence locations, (b) from the Random Forest (RF) based on the RS species occurrence locations, (c) from the Generalized Additive Linear Model (GAM) based on the remote sensing (RS) species occurrence locations and (d) from the Maximum (MaxEnt) Model based on the RS species occurrence locations.

Appendix I

Table A3: Ecological niche modelling performances. The GAM and MaxEnt rows for the Field columns are NA because the TSS and AUC from these were less than 0.7 and 0.8 so we excluded these models from the analysis.

Parameters						
Model	**AUC**		**Threshold**		**TSS**	
	Field	**RS**	**Field**	**RS**	**Field**	**RS**
EM	0.982	0.961	564.833	634.417	0.885	0.805
GAM	NA	0.943	NA	572.540	NA	0.789
RF	0.982	0.968	570.875	675.625	0.881	0.811
MaxEnt	NA	0.928	NA	634.167	NA	0.730

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9 Appendix

Appendix 1

While creating this dissertation, I have also contributed to the following publications which were not included in this thesis:

Beierkuhnlein, C., Field, R., Nogales, M., Veetas, O. R., Walentowitz, A., **Weiser, F.**, Stahlmann, R., Guerrero-Campos, M., Jentsch, A., Medina, F., Chiarucci, A., (2023) *Volcanic ash deposition as a selection mechanism towards woodiness* [Manuscript submitted for publication], Department of Biogeography, University of Bayreuth

Biurrun, I., Pielech, R., Dembicz, I., Gillet, F., Kozub, Ł., Marcenò, C., …, **Weiser, F.**, ... & Nobis, M. (2021). Benchmarking plant diversity of Palaearctic grasslands and other open habitats. *Journal of Vegetation Science*, *32*(4), e13050.

Dengler, J., Wagner, V., Dembicz, I., García-Mijangos, I., Naqinezhad, A., Boch, S., ... **Weiser, F.**, …. & Talebi, A. (2018). GrassPlot–a database of multi-scale plant diversity in Palaearctic grasslands.

Friedl, P., **Weiser, F**., Fluhrer, A., & Braun, M. H. (2020). Remote sensing of glacier and ice sheet grounding lines: A review. *Earth-Science Reviews*, *201*, 102948.

Nogales, M., Guerrero-Campos, M., Boulesteix, T., Taquet, N., Beierkuhnlein, C., Campion, R., Fajardo, S., Zurita, N., Arechavaleta, M., García, R., **Weiser, F.**, & Medina, F. M. (2022). The fate of terrestrial biodiversity during an oceanic island volcanic eruption. *Scientific Reports*, *12*(1), 1-12.

Schuldt, B., Buras, A., Arend, M., Vitasse, Y., Beierkuhnlein, C., Damm, A., ..., **Weiser, F.**, … & Kahmen, A. (2020). A first assessment of the impact of the extreme 2018 summer drought on Central European forests. *Basic and Applied Ecology*, *45*, 86-103.

Appendix 2

Table A1: List of scientific presentations

Conference	**Organization**	**Date and Location**	**Title**	**Type**
Jahrestagung	Arbeitskreis Biogeographie im Verband der Geographen an deutschen Hochschulen	05/2017 Erlangen	Reaktion von Baumgrenzen in Abisko, Schweden, auf Fraßschäden durch *Epirrita autumnata* Massenvorkommen	Poster
Interdisziplinäre Wissenschaftstagung zur Biodiversitätsforschung im Rahmen des UN-Übereinkommens über die biologische Vielfalt (CBD)	Bundesamt für Naturschutz (BfN)	08/2017 Vilm	Reaktion von Baumgrenzen in Abisko, Schweden, auf Fraßschäden durch *Epirrita autumnata* Massenvorkommen	Oral
Biodiversität und Klima - Vernetzung der Akteure in Deutschland	Bundesamt für Naturschutz (BfN)	11/2017 Vilm	Reaktion von Baumgrenzen in Abisko, Schweden, auf Fraßschäden durch *Epirrita autumnata* Massenvorkommen	Oral
Living Planet Symposium	European Space Agency (ESA)	05/2019 Milan	Forest Reactions to the Summer 2018 in Northern Bavaria, Germany- Monitoring Drought from Space	Poster
Deutscher Kongress für Geographie 2019	Deutsche Gesellschaft für Geographie (DGfG)	09/2019 Kiel	How did forests in Northern Bavaria react to the summer drought 2018? A remote sensing approach	Poster
BayCEER Workshop 2019	BayCEER	10/2019 Bayreuth	Using Sentinel 2 to analyze the spatial distribution of damage after the 2018 summer drought	Oral
1.Netzwerktreffen	Bayrisches Wissenschaftsforum (BayWISS)	11/2019 Freising	Using Sentinel-2 to analyze the spatial distribution of	Poster

			damage after the 2018 summer drought	
10th Biennial Conference	International Biogeography Society (IBS)	06/2022 Vancouver	Impacts of forest fire on understory species diversity in Canary Pine ecosystems on the island of La Palma	Oral
BayCEER Workshop 2022	Bayreuth Center of Ecology and Environmental Research (BayCEER)	10/2022 Bayreuth	Impact of volcanic sulfur and ash emission on the flora of La Palma, Spain	Oral
SFE²-GfÖ-EEF joint meeting Metz 2022	The Ecological Society of Germany, Austria and Switzerland (GFÖ)	11/2022 Metz	Impact of volcanic sulfur emissions on the pine forest of La Palma, Spain	Poster

Appendix 3

Table A2: Contributions to non-peer reviewed publications (Asteriks mark equal contributions)

Newsletter, journal or bulletin	Publisher	Title	Authors
Tuexenia, *36*, 337-358 (2016)	Floristisch-sozilogische Arbeitsgemeinschaft e.V.	Diversity and functional composition of alpine grasslands along an elevational transect in the Gran Paradiso National Park (NW Italy)	Baumann, E.*, **Weiser, F.*,** Chiarucci, A., Jentsch, A., Dengler, J.
Bulletin of the Eurasian Dry Grassland Group, *31*, 12-26. (2016)	European Dry Grassland Group (EDGG)	Scale-dependent plant diversity in Palaearctic grasslands: a comparative overview	Dengler, J., Biurrun, I., Apostolova, I., Baumann, E., Becker, T., Berastegi, A., ... & **Weiser, F.**
BfN-Skripten 497 (2018)	Bundesamt für Naturschutz (BfN)	Reaktion von Baumgrenzen in Abisko, Schweden, auf Fraßschäden durch Epirrita autumnata-Massenvorkommen	**Weiser, F.**
Forum der Geoökologie, 2, 21-25 (2018)	Verband für Geoökologie in Deutschland e.V. (VGöD)	Fernerkundung zur exakten räumlichen und zeitlichen Analyse der Effekte von Waldbränden im	**Weiser, F.,** Beierkuhnlein, C.

		Kanarenkiefernwald von La Palma	
The ever growing use of Copernicus across Europe's regions - A selection of 99 user stories by local and regional authorities	Copernicus	Enabling earth observation for protected areas	Lucas, R., Blonda, P., Bustamante, J., Diaz-Delgado, R., Giamberini, S., Kordelas, G., Gonçalves, J., Manakos, I., Santoro, M.,Sonnenschein, R., **Weiser, F.**, Willm, L., Viterbi, R.

Appendix 4

During the time working on this thesis, I reviewed a manuscript submitted to the journal *Ecology and Evolution*

10 Eidesstattliche Versicherungen und Erklärungen

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit versichere ich eidesstattlich, dass ich die Arbeit selbstständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe (vgl. Art. 64 Abs. 1 Satz 6 BayHSchG).

(§ 8 Satz 2 Nr. 3 PromO Fakultät)

Hiermit erkläre ich, dass ich die Dissertation nicht bereits zur Erlangung eines akademischen Grades eingereicht habe und dass ich nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden habe.

(§ 8 Satz 2 Nr. 4 PromO Fakultät)

Hiermit erkläre ich, dass ich Hilfe von gewerblichen Promotionsberatern bzw. –vermittlern oder ähnlichen Dienstleistern weder bisher in Anspruch genommen habe noch künftig in Anspruch nehmen werde.

(§ 8 Satz 2 Nr. 7 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass die elektronische Fassung der Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung unterzogen werden kann.

(§ 8 Satz 2 Nr. 8 PromO Fakultät)

Hiermit erkläre ich mein Einverständnis, dass bei Verdacht wissenschaftlichen Fehlverhaltens Ermittlungen durch universitätsinterne Organe der wissenschaftlichen Selbstkontrolle stattfinden können.

…………………………………………………………………………………….

Ort, Datum, Unterschrift