

MADLI JÕKS

Biodiversity drivers in oceanic
archipelagos and habitat fragments,
explored by agent-based simulation
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UNIVERSITY OF TARTU
Press

Department of Botany, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in botany and mycology at the University of Tartu on April 10th, 2023, by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 127, J. Liivi 2, Tartu, on May 26th, 2023, at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479 (print)

ISBN 978-9916-27-194-0 (print)

ISSN 2806-2140 (pdf)

ISBN 978-9916-27-195-7 (pdf)

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University of Tartu Press
www.tyk.ee

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers denoted in the text by Roman numerals:

- I** **Jõks, M.** and Pärtel, M. 2019. Plant diversity in Oceanic archipelagos: realistic patterns emulated by an agent-based computer simulation. – *Ecography* 42: 740–754.
- II** **Jõks, M.**, Kreft, H., Weigelt, P., Pärtel, M. 2021. Legacy of archipelago history in modern island biodiversity – An agent-based simulation model. – *Global Ecology and Biogeography* 30: 247–261.
- III** **Jõks, M.**, Helm, A., Kasari-Toussaint, L., Kook, E., Lutter, R., Noreika, N., Oja, E., Öpik, M., Randlane, T., Reier, Ü., Riibak, K., Saag, A., Tullus, H., Tullus, T., Pärtel, M. 2023. A simulation model of functional habitat connectivity demonstrates the importance of species establishment in older forests. – *Ecological Modelling* 481: 110361.

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Author's contribution to the publications:

- I, II, III** participated in developing the idea and simulation script writing, had the main responsibility in simulation experiments, data analyses and manuscript writing.

1. INTRODUCTION

Islands are considered perfect ecological study systems due to their distinct physical boundaries and resulting well-defined populations. Evolutionary curiosities, high endemism rates, and disproportionate contribution to the global biodiversity loss add to reasons why islands have attracted ecologists' attention for centuries. Among them, oceanic islands of volcanic origin, that have never been connected to the mainland, offer a special opportunity to study biodiversity development in action, driven by the immigration and evolution processes (Whittaker and Fernández-Palacios 2007, Warren et al. 2015). In addition, oceanic archipelagos act as networks of directional species dispersal, driven by spatio-temporal dynamics. Intriguingly, fragmented habitats within landscapes, that are mostly a result of human activity, function somewhat similarly to real archipelagos and offer an equally interesting opportunity to study the dynamics of spatially isolated populations, as well as an equally important conservational challenge.

The equilibrium theory of island biogeography, first proposed by MacArthur and Wilson in 1963, replaced the until-then dominated static view on oceanic islands with dynamic equilibrium and quickly claimed the role of leading paradigm among island ecologists. It elegantly connected two defining processes – immigration and extinction – with their principal limiting factors – isolation and area respectively – into a simple model. Theory states that as both processes depend on the number of species already present on the island, a dynamic equilibrium between immigration and extinction occurs after some time, resulting in a more or less steady number of species with changing assembly. This dynamic view on local species composition laid the foundation for the concept of species pool, which is defined as the set of all species available to colonize a focal site (Cornell and Harrison 2014) and has been later widely developed and discussed in ecology (Zobel 2016).

During the following decades the equilibrium theory was tested and proved on several different systems (reviewed by Schoener 2010), but also challenged and criticized for its limitations. Several authors have argued that the assumption of island ever getting to the equilibrium state is false, as volcanically active islands are constantly disrupted by new explosions (Bush and Whittaker 1993, Heaney 2000). It has been also demonstrated that immigration is not only limited by island isolation, as stated by MacArthur and Wilson, but can be also affected by island area (target area hypothesis, Gilpin & Diamond, 1976) and extinction is not only limited by island area but also by island isolation (rescue hypothesis, Brown & Kodric-Brown, 1977). Whittaker et al. (2008) argued that MacArthur and Wilson's theory is unfit for oceanic islands, where evolution contributes at the same time scales as immigration to the species richness increase. In addition, the lack of several other factors – habitat diversity, archipelagic configuration, and geological development – have been pointed out (e.g. Heaney 2000, Whittaker et al. 2008). General dynamic theory of oceanic island biogeography (Whittaker

et al. 2008) ties the rates of immigration and extinction as well as the local speciation to the life cycle of a typical hotspot oceanic island, which emerges from the sea, builds to the maximal area and height, and then starts eroding and subsiding. The peak of local speciation approximately cooccurs with the topographic complexity in the island's 'middle age' shortly after the maximal elevation and area have been passed, and species richness forms a hump-shaped relationship with island age.

Despite the shortcomings, MacArthur and Wilson's theory of island biogeography undeniably became a paradigm and a starting point for every island biogeography study to be published in coming decades. Even more, for a while it also dominated the entire spatial ecology: it was quickly adopted as the primary model to study the 'habitat islands' of the fragmented landscapes. By the early 1980s, it had become the dominant ecological paradigm in conservation biology (Hanski and Simberloff 1997) and it was even used as a basis for the best spatial configuration of nature reserves (Diamond 1975, Terborgh 1975, Hanski 2001). However, by the end of the decade, its popularity was declining both in ecology and in conservation biology, while conceptually close metapopulation theory, first introduced by Levins in 1969, began to gain popularity. Metapopulation, according to Levins, is a set of spatially separated subpopulations, which are connected by dispersing or migrating individuals. Each subpopulation is characterized by a high extinction probability, whereas the migrating individuals are buffering the entire metapopulation from being endangered by the small-scale environmental change. Similarly to island biogeography theory, metapopulation theory emphasizes the importance of spatial arrangement of individuals and populations and resulting ecological interactions (Hanski 1998). The main difference from island biogeography theory is the lack of mainland species pool and the occurrence of several small 'island' populations.

If first, landscape ecology had adopted elements from island biogeography, then in the 2000s, the latter started to look towards landscape ecology for the methods. One such aspect has been the island isolation metric, as MacArthur and Wilson's initial theory fails to cover the archipelagic organization of most oceanic islands. It has been pointed out that for real oceanic islands, older islands of the neighborhood are much more probable sources of species than the very distant mainland and thus, island isolation metric should not reflect only the distance to the mainland, but rather account for the entire spatial organization of the archipelago (Weigelt and Kreft 2013). Thus, several alternative isolation metrics have been tested, e.g. distance to the nearest older island (Cardoso et al. 2010), distance to the center island of the archipelago (Willerslev et al. 2002), mean distance to other islands (Borges and Hortal 2009), the availability of mainland in the surrounding of the island (Weigelt and Kreft 2013), distance to the climatically similar landmass (Price 2004, Weigelt and Kreft 2013) as well as the dispersal ability of the mainland species pool (Cabral et al. 2019a).

Although real and habitat islands share several properties, there is also a crucial difference between the two. While ocean around the islands is considered a totally unfit habitat for terrestrial species, this binary habitat/nonhabitat classi-

fication may not apply for habitat fragments, such as old-growth forests (Kupfer et al. 2006). Forest fragmentation is a global conservation concern, resulting in small and isolated populations of forest-specific biodiversity. Estonian old stable forest fragments are no exception, being surrounded by the areas of non-forest and anthropogenic habitats, but also by younger secondary forests which have mainly developed on abandoned agricultural land as a result of socio-economic changes. Whereas grasslands or anthropogenic landscapes might be totally uninhabitable for old-forest specific biodiversity, the secondary or managed forests might support it to some degree. Therefore, it is suggested that treating forest fragments as oceanic islands is unreasonable and instead, landscape around the forest patches (matrix) should be considered in its heterogeneity (Kupfer et al. 2006), while counting for the organisms' response to the landscape. For that purpose, functional connectivity, which describes organisms' ability to move among the patches (Tischendorf and Fahrig 2000), can be used in addition to the spatial arrangement – or the structural connectivity – of the patches. Moreover, for slowly or passively dispersing taxa, such as plants, lichens, fungi and even insects, functional connectivity might not solely depend on their ability to move among the patches, but also on their ability to establish temporary populations in the matrix. Similarly to island isolation, high connectivity between the habitat fragments leads to higher immigration rates and consequently, to higher species richness (Taylor et al. 1993, Rosenberg et al. 1997). Additionally, forest age has often been associated with habitat quality (reviewed by Nordén et al., 2014), but it is unsettled, how well the surrounding different-aged secondary forests support connectivity and biodiversity of the old-forest fragments.

Island biogeography has historically been dominated by descriptive research approach and correlational statistical models. A main shortcoming of correlational methods is their inability to identify causal relationships (Gotelli et al. 2009, Cabral et al. 2017, Hagen 2022) and therefore, process-based (mechanistic) models which dynamically simulate processes and resulting biodiversity patterns through the rules or equations that have biologically meaningful parameters, have been suggested as a more informative approach (Cabral et al. 2017). During the recent decades, using process-based models in island biogeography has greatly advanced (e.g. Rosindell and Phillimore 2011, Rosindell and Harmon 2013, Valente et al. 2015, Borregaard et al. 2016, Gascuel et al. 2016, Matthews et al. 2020, Aguilée et al. 2021) owing to the simultaneous progress in computational power and availability of spatial data. Agent-based simulations are process-based models that simulate populations and communities via discrete agents that represent individual organisms or groups of similar individual organisms (DeAngelis and Mooij 2005). In ecology, these models have been mostly used to study animal movement and behavior and thus, they have often been called individual-based simulations. Unlike the classical differential-equation models, agent-based models are based on relatively simple rules that apply to individual agents, which leads to system-level biodiversity patterns emerging bottom-up. A strategy called pattern-oriented modeling has been proposed for agent-based modeling, which focuses on reproducing the observed patterns of nature (Grimm et al. 2005). To

prevent a situation, where a single model is parametrized to fit empirical data regardless of its underlying processes, contrasting alternative models and their outcomes is suggested (Grimm et al. 2005).

Due to their obvious advantages for smaller-scale studies, where individual differences and spatial organization of individuals are of great importance, agent-based simulation models have been much more widely used in landscape and population ecology (e.g. Travis et al. 2005, Xiao et al. 2010, Kazmierczak et al. 2016) than in biogeography. For example, forest gap models which simulate the establishment, growth and mortality of individual trees as a function of competition and abiotic factors, have been developed since the 1960s (e.g. Botkin et al. 1972). Individual-based models have been also often used to study forest connectivity, but these studies have mostly considered active animal movements, behavior, and habitat selection (e.g. Trapp et al. 2019, Zeller et al. 2020, Rohwäder and Jeltsch 2022). However, agent-based models can be a helpful tool to study connectivity of passively dispersing organisms, as well as for larger-scale studies of biogeography and macroecology due to their clearly mechanistic, stochastic, and spatially explicit nature and relatively easy and intuitive parametrization. Gotelli et. al (2009) suggest that simulation approach for modeling large-scale species distributions in macroecology helps to deal with challenges of spatial autocorrelation, inter-correlated predictor variables, nonlinear responses of species richness to environmental variables and effects of spatial scale, imposed by traditional curve-fitting methods.

In this thesis, I used spatially explicit mechanistic agent-based simulation models to study biodiversity drivers on real (oceanic) islands as well as in Estonian old-forest fragments.

The main objectives of the thesis were:

1. to explore the ability of relatively simple agent-based simulation models to emulate realistic biodiversity patterns and their potential for biogeography and landscape ecology research (**I, II, III**);
2. to disentangle the effects of habitat diversity and archipelago configuration from the effect of island area on biodiversity development in oceanic archipelagos (**I**);
3. to study the imprint of geological and eustatic histories of oceanic archipelagos in their modern biodiversity (**II**);
4. to assess the functional connectivity (or insularity) of the old-forest fragments (**III**);
5. to determine which process (establishment and / or survival) is limiting the old-forest specific biodiversity from exploiting the younger forests between the old-forest fragments (**III**).

2. MATERIALS AND METHODS

2.1. Study areas

All archipelagos used in papers **I** and **II** (Hawaiian Islands, Canary Islands and Galápagos Islands in both papers, and Azores and Cape Verde only in paper **I**) are volcanic hotspot archipelagos. In hotspot archipelagos, tectonic plate motions that carry older islands further away from the mantle plume where new islands emerge, cause different-aged islands to follow each other in age-progressive configuration (Wilson 1963). This, in turn, causes intra-archipelagic dispersal to occur mostly from older to younger islands, and thus, the sequence of colonization of a species group to correspond to the geological ages of islands (known as the progression rule; Funk and Wagner 1995). Hawaii probably represents the most typical example of such stepping-stone pattern, as the islands are very linearly spaced in the archipelago. However, even there the pattern is confounded by the historical fusions and splittings of the islands due to geological developments as well as by the eustatic sea level fluctuations (Price 2004, Price and Elliott-Fisk 2004), and in other archipelagos, the pattern is even less clear. The archipelagos differ significantly in their age, with the oldest of modern Canary Islands being over 20 million years old (Fernández-Palacios and Whittaker 2008) whereas the oldest present-day island of Galápagos archipelago emerged approximately 3 million years ago (Geist et al. 2014).

In paper **III**, I used Estonian fragmented old-growth nemoral forests as a system of insular habitat patches. In Estonia, two forest types prevail: boreal and nemoral forests. Nemoral forests which occur in southern Sweden and east of the Baltic Sea (Metzger et al. 2005) are characterized by neutral to alkaline nutrient rich soils and broad-leaved deciduous trees. They are the most species rich forests of the region, while their species composition significantly differs from the boreal forests (Noreika et al. 2019). In Estonian landscape, old-growth nemoral forests occur as habitat fragments, surrounded by different-aged secondary nemoral and boreal forests and by other natural and anthropogenic ecosystems.

2.2. Biodiversity and abiotic environmental data

In all three papers, using a pattern-oriented modeling approach, simulated data of different scenarios were compared against the empirical data to define scenarios (implemented factors and processes, parameter values) that resulted in most realistic biodiversity patterns. Empirical data from oceanic islands and from 32 Estonian forest sites were used.

For oceanic islands, native species lists of Spermatophyta and Pteridophyta (**I** and **II**) and Passeriformes, Lepidoptera and Coleoptera (**II**) were used from several literature sources (Nishida 2002, Izquierdo et al. 2004, Arechavaleta et al. 2005, 2009, Silva et al. 2005, Boyer 2008, Imada 2012, Jaramillo Díaz and Guézou 2013, Jiménez-Uzcátegui et al. 2014, Illera et al. 2016, Peck 2017, Roque-Álbelo

and Landry 2018, Weigelt et al. 2020). In addition, either the Jaccard similarity index between the islands (**I**) or proportion of single-island endemics on each island (**II**) was used.

For Estonian nemoral forest sites (**III**), I used species richness numbers of different functional groups (ground diversity, epiphytes, ectomycorrhizal (EcM) fungi, arbuscular mycorrhiza (AM) fungi, saprotrophic and pathogenic fungi, woody plant diversity, carabid beetles) and empirical abiotic data (soil NPK, soil pH, mean annual temperature, precipitation, spatial coordinates) by Noreika et al. (2019).

2.3. Spatial input data

Empirical landscapes of the oceanic islands and around the forest study sites were represented as raster maps in the simulations. For oceanic archipelagos, I derived present archipelago maps from elevation–bathymetry raster maps (Amante and Eakins 2009, Danielson and Gesch 2011) where one raster cell represented an area of $0.0167^\circ \times 0.0167^\circ$ (2–3 km², depending on the latitude of the archipelago). These realistic present-day maps were modified in different simulation scenarios in several ways. In paper **I** and **II**, island cells were classified into 5–6 habitat types based on their mean elevation. In some scenarios of paper **I**, I deleted any habitat diversity (all elevations were defined as habitat type 1) to test the effect of habitat diversity. Islands were also shuffled around in the convex hull of the archipelago or in a circle with a diameter equal to the largest extent of the archipelago to test the effect of archipelago spatial configuration (Figure 1). In paper **II**, I reconstructed greatly simplified geological histories of Hawaii, Galápagos, and Canary Islands, by creating dynamic simulations where each 0.5 Myr was represented by one map that was used for 50 simulation cycles. Simulations started with the emergence of the oldest present-day islands and ended with the modern map – thus using 41 maps for the Canary Islands, 10 for Hawaii and six for Galápagos. Islands emerged in chronological order and increased and decreased in size and elevation during the simulation (Figure 2). In addition, I reconstructed eustatic histories of the same archipelagos, by combining the elevation–bathymetry maps (Amante and Eakins 2009) with historical global sea-level reconstructions (Bintanja et al. 2005). I derived a map for every 10 000 years, which resulted in 100 maps for the last 1 Myr (sea level between 0 and 130 m below present level).

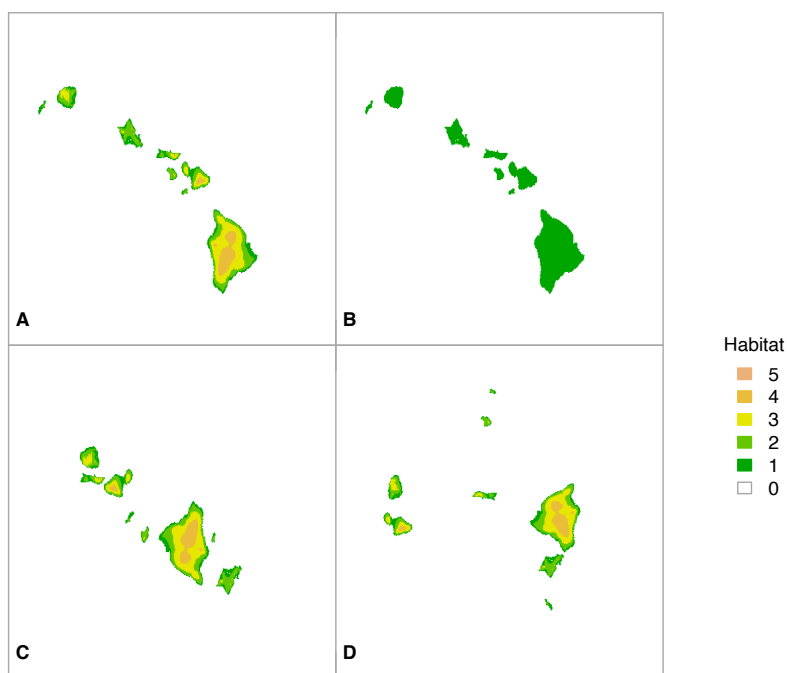


Figure 1. An example of simulation map alterations to study the effect of habitat diversity and archipelago configuration. Hawaiian archipelago with real configuration and habitat diversity (A), real configuration without habitat diversity (B), with convex hull randomization (C) and with circle randomization (D). Modified from paper I.

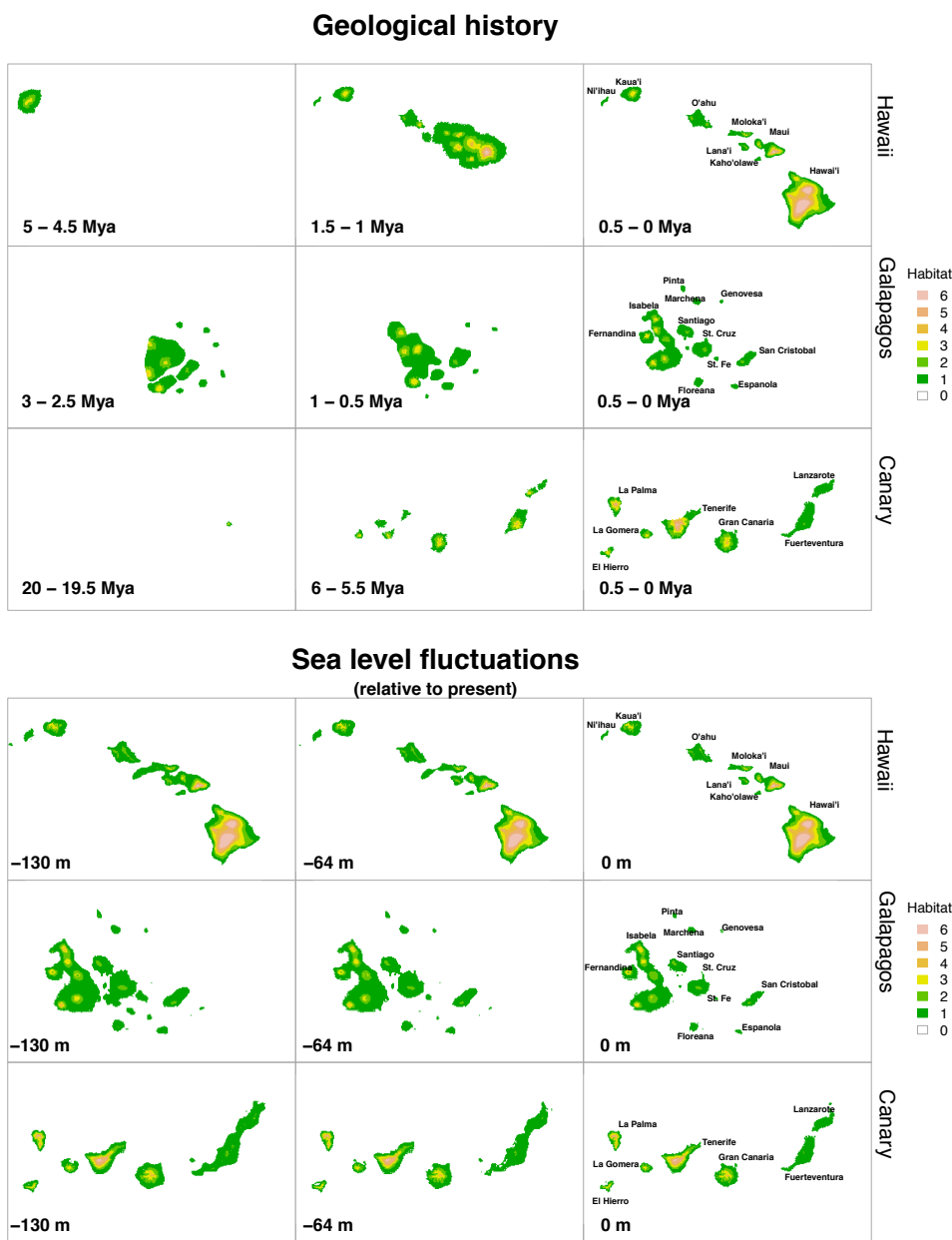


Figure 2. Three illustrative stages of geological history and sea-level fluctuation simulation scenarios in all studied archipelagos. Figure from paper II.

For Estonian nemoral forest plots (III), I combined four mappings of forested land (from the 1900s, 1940s, 1970s and 2010s) into static maps of different-aged nemoral forests in 5 km radius circles around the old-growth nemoral forest study sites. In this study, one raster cell represented an area of 100×100 m. Similarly to translating island elevation into habitats in paper I and II, here forest occur-

rence in different decades was translated into forest age class. Areas that were classified as forested land only on the map of 2010 were defined as the youngest forests (“Age1”); forested land that was present on the maps of 2010 and 1970s – “Age2”; 2010 and 1940s – “Age3”; 2010s and 1900s – “Age4”. All habitats other than nemoral forests were defined as 0, where nemoral forest-specific species couldn’t survive (Figure 3).

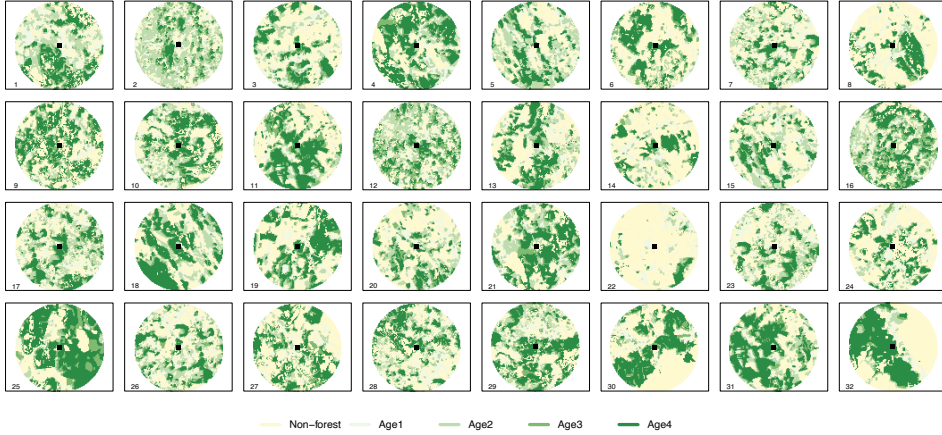


Figure 3. Simulation maps with four forest-age classes and uninhabitable matrix, representing the empirical landscapes in the 5 km radius surrounding the 32 Estonian nemoral forest sites (black cells in the center) where the observed diversity data of several functional groups were collected. Maps are ordered according to the mean rank of observed species richness of all studied groups (increasing from top left to bottom right). Figure from paper **III**.

2.4. Simulation model

I simulated the dynamics of subpopulations of virtual species either on and among the oceanic islands or in a 5 km radius circle around the old-growth nemoral forest study sites, using empirical landscapes. In papers **I** and **II**, immigration, establishment, dispersal, mortality, and speciation processes were simulated. In paper **III**, simulations operated on ecological timescale, thus excluding speciation but including immigration, establishment, dispersal, and mortality. In all three papers, I then compared simulated diversity of virtual species to the observed diversity of different biodiversity groups to find which simulation scenarios result in the values that have highest correlations with the empirical data. I did not parameterize the model separately for each functional group but correlated the simulated species richness of the virtual species to the observed species richness of each group to find parameter values that best fit each group (pattern-oriented approach, see section 2.5.).

The stochastic, spatially explicit agent-based simulation model, written in R programming language (R Core Team 2022) simulated dynamics and interactions

of subpopulations of virtual species, using raster maps as simulation arena (see section 2.3.). The operating agent of the model was a subpopulation of a virtual species. Each cell was described by two state variables: habitat type and whether it was empty or inhabited. In papers **I** and **II**, subpopulations were described by their position, species identity, species-specific genome, and species-specific phenotype. In that case, randomly generated composition of the genome determined the species dispersal and establishment ability. All subpopulations of the same species were identical (no intraspecific variation) but did not act identically due to stochastic variation. In paper **III**, only one species was simulated at a time, and subpopulations were characterized only by their position. Spatial scale of the simulation frame varied from about 78 km² (7843 cells) in paper **III** to on average about 150 000 km² in papers **I** and **II** (about 6000 cells).

Each simulation run was initialized with empty islands in papers **I** and **II** or with all forest cells occupied by a single species in paper **III**. The simulation proceeded in distinct time steps. At each time step, some subpopulations immigrated from outside, established a cell, reproduced, dispersed, and died. In papers **I** and **II**, some subpopulations also evolved into a new species. Number of time steps varied between 100 (**III**) and 2050 (**II**). One time step represented approximately a year in paper **III** and 10 000 years in paper **II**. In paper **I**, time step did not have an explicit meaning.

In papers **I** and **II**, several species were simulated together and mainland species pool of 100 species was included; in paper **III**, one species was simulated at a time and results of 1000 runs were stacked to obtain simulated species richness of virtual species.

Simulation model consisted of several parts, which were run sequentially: immigration, establishment, reproduction together with dispersal, and mortality / survival. Below, these submodels are described.

Immigration: In all scenarios of all papers, at each time step, 10% of the cells received immigrants. That simulated either the arrival from mainland (in **I** and **II**) or from outside of the 5 km radius area in paper **III**. Immigration was non-directional with all cells having equal probability of receiving the immigrants.

Establishment: A subpopulation established an unoccupied cell with the probability determined by the simulation variation and scenario. It varied between 10% and 100%.

Reproduction and dispersal: In all scenarios of all papers, at each time step 40% of all subpopulations (randomly chosen) tried to send a descendant to another cell. Dispersal distance was either dependent on the genome (**I** and **II**) or generated randomly (**III**) but was always described by a negative binomial dispersal kernel and varied randomly due to stochasticity. As a result, most dispersal events occurred quite close to the initial subpopulations and only a few reached longer distances.

Mortality / Survival: At each time step, some subpopulations were randomly removed. The number of removed subpopulations depended on the simulation variation and scenario. Mortality varied between 10% and 25%, while the remaining 75% to 90% subpopulations survived.

Speciation: In papers **I** and **II**, at each time step, 0.1% of the subpopulations evolved into a new species by a random change in their genome. Only species that were present on the islands were able to evolve, whereas species in the initial species pool remained unchanged. In paper **III**, no speciation was implemented.

2.5. Experimental design

In all three papers, different simulation scenarios were contrasted to define crucial factors in biodiversity pattern development:

- in paper **I**, habitat diversity (no diversity vs diversity) and archipelago spatial configuration (real configuration, convex hull randomization and circle randomization) were used (Figure 1);
- in paper **II**, one factor in four levels (degree of included historical data: no archipelago history, eustatic history, geological history or both combined) was used (Figure 2);
- in paper **III**, eight by eight (altogether 64) survival and establishment scenarios were used, which differed in how much they favored older forests over younger ones (Figure 4).

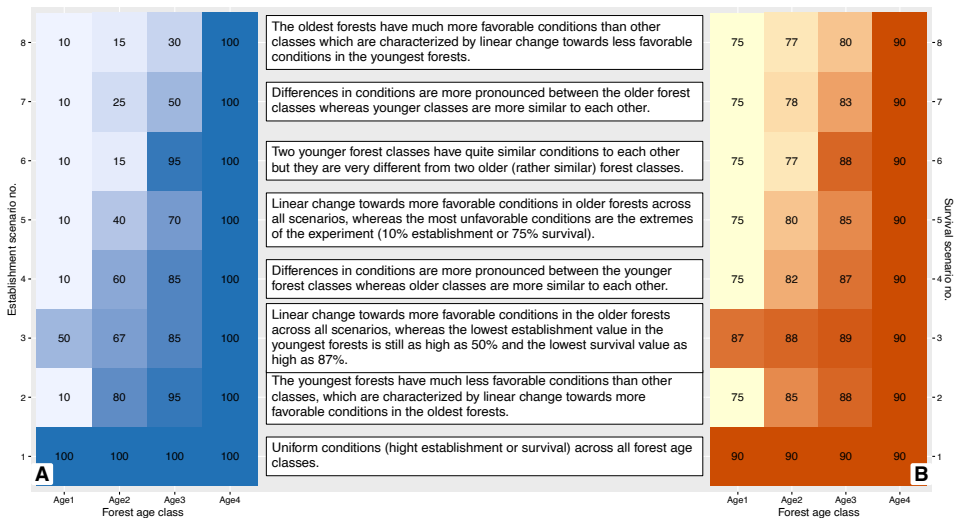


Figure 4. Establishment (A) and survival (B) rates (%) in eight establishment and eight survival scenarios of Estonian nemoral forest simulations. Color intensity indicates the probability of the process. Higher scenario number generally indicates greater differences between the forest-age classes in establishment or survival value (thus, stronger affinity for older forests). Each establishment value was combined with every survival value. Scenarios of both parameters follow a common logic and thus the text explanations apply for both. Figure from paper **III**.

2.6. Statistical analyses

In all three papers, I derived simulated diversity data at the end on the simulation runs and calculated correlations between simulated and observed data. In papers **I** and **II**, mean species richness of the final 50 cycles on each island, and either compositional dissimilarity among the islands (Jaccard index, paper **I**) or the proportion of single-island neo-endemics (paper **II**) at the end of the simulation were used. In paper **III**, simulated species richness was obtained by assessing the frequency of inhabited central study cell over the 1000 simulation runs.

In papers **I** and **II**, correlations between the log-transformed observed and simulated species richness numbers were then found. In addition, either Spearman correlations between observed and simulated Jaccard index matrices (paper **I**) or between logit-transformed observed and simulated proportions of single-island endemics (paper **II**) were found.

In paper **III**, to remove the effects of environmental factors and spatial autocorrelation, I first calculated the residuals to the linear models, where empirical or simulated species richness was the dependent variable and environmental factors and / or spatial parameters were the independent variables, and then correlated the residuals.

In all cases, after applying Fisher's z-transformation to the correlation coefficients, I used them as dependent variables in linear models to determine the effect of the simulation scenario on the correlation strength. To understand the pairwise differences between the scenarios, I also conducted post hoc comparisons on the model results. In paper **II**, to determine which islands caused the differences in correlation strength between the simulation scenarios, I also conducted a residual analysis for each simulation run: after standardizing simulated and observed species richness, I calculated residuals from the perfect correlation (i.e., intercept=0, slope=1).

3. RESULTS

3.1. Accordance between the simulated and observed biodiversity

In papers **I** and **II**, simulated species richness had strong positive correlations with observed species richness in most cases (Figure 5 and Figure 6). Strongest correlations generally emerged for Hawaii (mean across the species groups was around 0.87 in both papers) and the weakest for Canary Islands (0.25 in paper **I**, 0.72 in paper **II**). Mean correlations for compositional dissimilarity (**I**) varied greatly among archipelagos (from 0.01 for Canary Islands to 0.64 in Hawaii). Mean correlations between simulated and observed proportion of single-island endemics (**II**) varied between 0.44 (Hawaii) and 0.48 (Canary Islands) (Figure 7).

In paper **III**, positive correlations were obtained for ground layer and epiphytic vegetation as well as for EcM, saprotrophic, and pathogenic fungi at least in some scenarios (Figure 8). Mean correlations varied from 0.03 in pathogenic fungi to 0.41 in EcM fungi and respective maximum correlations from 0.21 to 0.52. Woody plants, carabid beetles and AM fungi mostly resulted in negative correlations, suggesting that these groups are more dominant in other habitats than forest.

3.2. Island habitat diversity affects species richness and composition in all studied archipelagos, whereas archipelago configuration affects species composition mainly in elongated archipelagos

Habitat diversity significantly increased simulation ability to emulate realistic patterns of species richness and species composition of spermatophytes and pteridophytes in all archipelagos (Figure 5 A, B, E, F). Archipelago configuration had a significant effect on the correlation between simulated and observed compositional dissimilarity in more elongated archipelagos of Hawaii and Azores (Figure 5 G, H). There, real archipelago configuration gave significantly stronger correlations than circle randomization either for both plant species groups (Hawaii) or only for pteridophytes (Azores). In Canary Islands, a significant difference between real configuration and convex hull randomization emerged, but not between real configuration and circle randomization (Figure 5 G).

3.3. In Hawaii and Galápagos, archipelago geological and eustatic histories have both affected species richness and proportion of single-island endemics

In Hawaii and Galápagos, simulation scenarios with more historical information generally increased correlations between simulated and observed biodiversity data. For the species richness of most studied Hawaiian taxa, the scenario with only geological history performed significantly better than the scenario with only eustatic history, and the combined scenario performed significantly better than any other (Figure 6). For the single-island endemics of Hawaii, the historical scenarios performed rather equally, except for spermatophytes, where both scenarios which included geological history performed slightly better than the scenario with only eustatic history (Figure 7). In Galápagos, the effect of implementing only eustatic history was mostly insignificant (except for the species richness of Lepidoptera); implementing only geological history had some effect (on the species richness of Passeriformes, Lepidoptera and Pteridophyta and on the proportion of single-island endemics of Coleoptera and Spermatophyta), but the combined scenario performed better than the present-day map in almost all cases (except for the single-island endemics of Lepidoptera) (Figure 6 and Figure 7). In Canary Islands, implementing geological history always significantly decreased simulation performance (Figure 6 and Figure 7). Implementing only eustatic history had no effect on species richness but had a significant positive effect on proportion of single-island endemics of Coleoptera and Spermatophyta (Figure 7).

Results of the residual analyses revealed that in Hawaii, implementing archipelago history generally reduced overestimations of species richness and single-island endemics on the island of Hawai'i and respective underestimations on Maui, Molokai, Oahu, and Kauai. In Galápagos, implementing history reduced the overestimations on Isabela and underestimations on St. Cruz. In the Canary Islands, implementing history increased the overestimations of the proportion of single-island endemics on Fuerteventura and Lanzarote and of species richness on Fuerteventura.

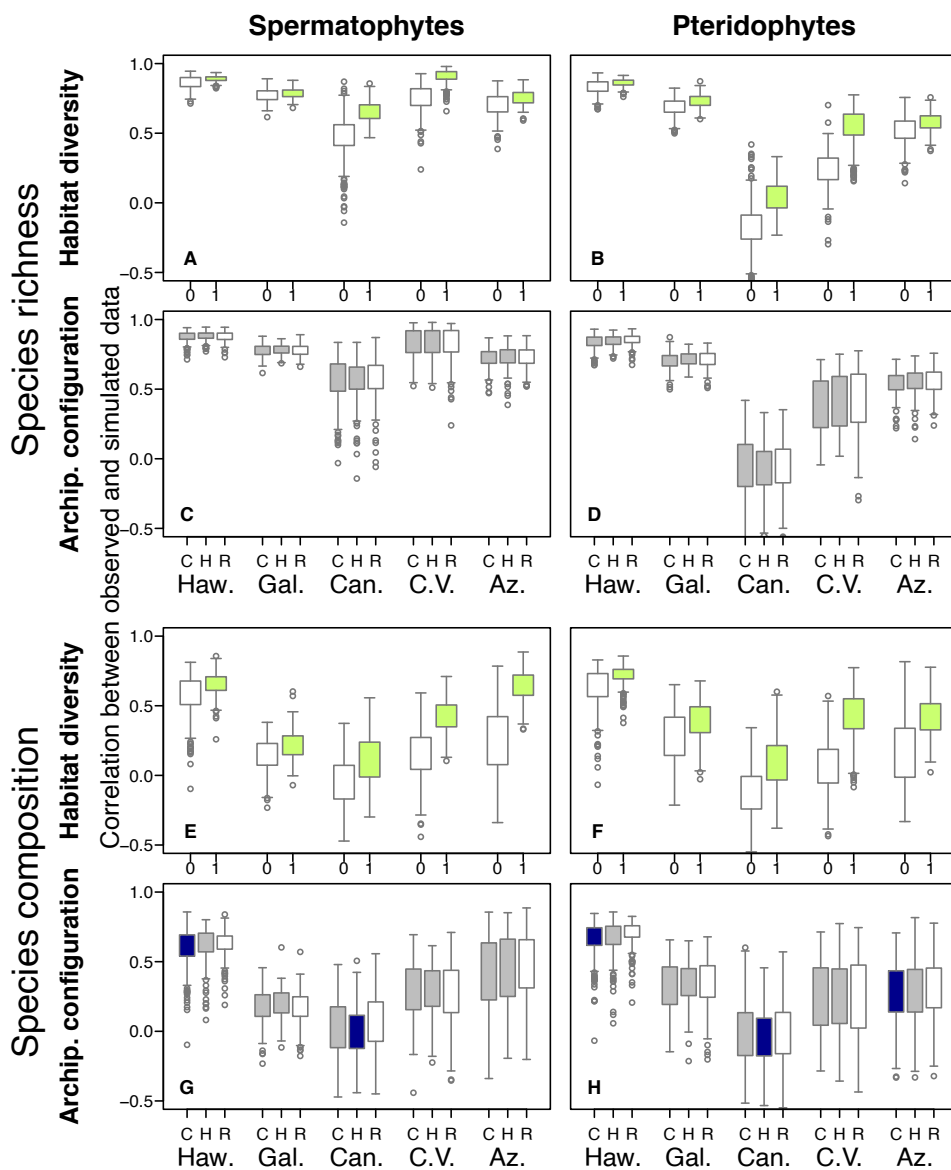


Figure 5. Effects of habitat diversity (A,B,E,F) and archipelago composition (C,D,G,H) on species richness (A–D) and species composition (E–H) of spermatophytes and pteridophytes. White bars indicate correlations without habitat diversity ('0') or with real configuration (R). If habitat diversity significantly increases the correlation (post hoc pairwise comparisons), the second bar ('1') is green. If circle ('C') or convex hull ('H') randomization significantly decreases correlations, respective bar is dark blue, otherwise grey. (Haw. – Hawaii, Gal. – Galápagos, Can. – Canary Islands, C.V. – Cape Verde, Az. – Azores). Figure from paper I.

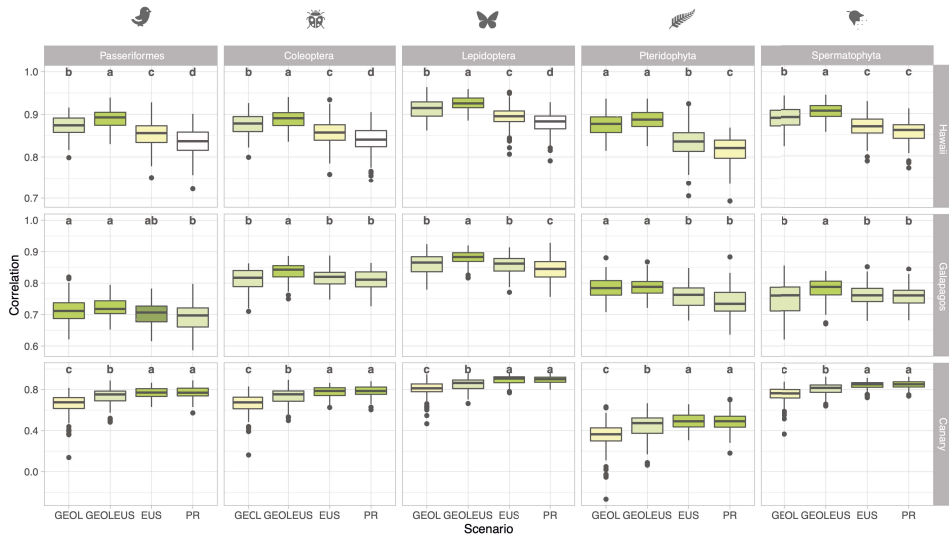


Figure 6. Effects of geological and eustatic history on correlations between simulated and observed species richness of Passeriformes, Coleoptera, Lepidoptera, Pteridophyta and Spermatophyta. Same letter (and box color) indicates no significant difference between the scenarios. (EUS = eustatic sea-level fluctuations; GEOL = geological history; GEOLEUS = geological history and eustatic sea-level fluctuations; PR = present map). Figure from paper II.

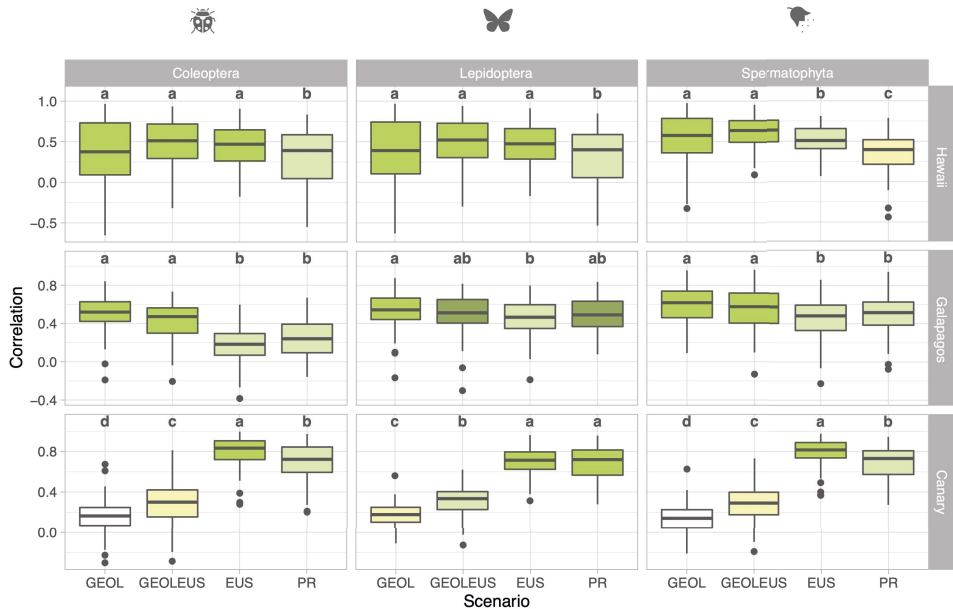


Figure 7. Effects of geological and eustatic history on correlations between simulated and observed proportion of single-island endemics of Coleoptera, Lepidoptera and Spermatophyta. Same letter (and box color) indicates no significant difference between the scenarios. (EUS = eustatic sea-level fluctuations; GEOL = geological history; GEOLEUS = geological history and eustatic sea-level fluctuations; PR = present map). Figure from paper II.

3.4. Estonian old-growth nemoral forest fragments are not functionally well connected by the younger secondary forests for several functional groups

In forest fragment simulations, most realistic species richness patterns of ground layer vegetation, epiphytes, EcM fungi and pathogens were achieved by the scenarios which defined large differences in establishment values between younger and older forests. Correlation strength culminated in the three most extreme scenarios with establishment values 10-15-95-100, 10-25-50-100 and 10-15-30-100 in different-aged forests (Figure 8 A–D). Common characteristic of all these three scenarios that distinguishes them from other five scenarios is the low establishment value in the second forest age-class, in approximately 40 – 50-year-old forests (see Figure 4). However, in saprotrophs, an opposite trend emerged: more differentiation between forest age classes resulted in weaker correlations and the strongest correlations were achieved in the scenario which treated all forests equal regardless of their age (Figure 8 E).

3.5. Establishment is the main limiting factor behind the old-forest affinity

Although establishment and survival rate both had significant effect on correlation strength between simulated and observed species richness across all functional groups, survival value had no significant effect on correlation strength in ground layer, epiphytes, or EcM fungi (Figure 8 F–H). Only in pathogens and saprotrophs, some differences emerged. For pathogens, survival scenario which defined equal survival values in all forest age classes, resulted in negative correlations, whereas in other scenarios correlations slightly increased (Figure 8 I). For saprotrophs, correlations decreased towards more differentiation between the forest age groups, similarly to the trend among the establishment scenarios (Figure 8 J). These results suggest dominance of establishment limitation over the survival limitation.

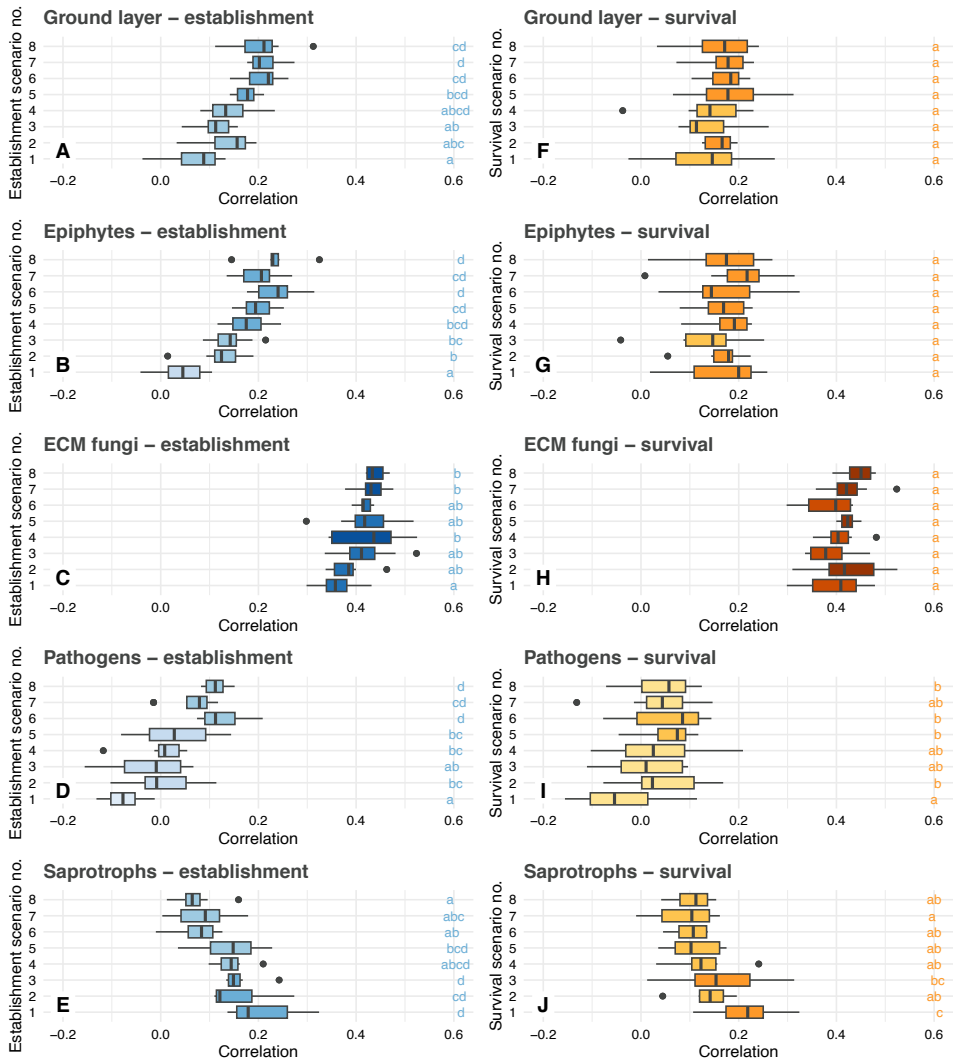


Figure 8. Effects of establishment (A – E) and survival (F – J) scenarios on correlations between simulated and observed species richness of different forest biodiversity functional groups. Higher scenario number generally indicates greater differences between the forest-age classes in establishment or survival value (thus, stronger affinity for older forests). Letters indicate the significant difference between the scenarios: scenarios that do not share a letter, differ significantly. Color gradient illustrates correlation strength. Figure from paper III.

4. DISCUSSION

Oceanic islands and habitat fragments share several common properties and therefore, landscape ecology and island biogeography have developed by inspiring each other. That much so, that leading theories of the two fields have been even called different aspects of the same, a more general model ('spatially realistic meta-population theory', Hanski 2001). Immigration and extinction dynamics, clear spatial distinction of the populations, as well as the conservation priority make both, real oceanic islands and habitat fragments, valuable study objects. The overall aim of this thesis was to explore the biodiversity drivers in these systems, that are characterized by the underlying effect of spatial and functional isolation.

Using agent-based simulations with pattern-oriented approach, I was able to emulate the emergence of realistic biodiversity patterns in oceanic archipelagos and in Estonian forests, and to gain knowledge of crucial processes behind these patterns. In paper I, simulation approach enabled me to disentangle the effects of habitat diversity and archipelago configuration from island area. In paper II, I was able to reconstruct the archipelago histories and in paper III, simulations helped me to gain mechanistic knowledge of processes behind the old-forest affinity. All these tasks are hard to achieve via field studies or statistical methods alone. In my thesis I showed that passive dispersal can successfully be studied with the help of agent-based models and that due to their clearly mechanistic, stochastic, and spatially explicit nature, they are a useful tool for both large-scale biogeography studies as well as for smaller-scale landscape ecology.

In papers I and II, I explored the factors that affect biodiversity development in oceanic hotspot archipelagos, thereby taking a step forward from island area and isolation. Although the relatively high overall correlations between simulated and observed data in both island studies indirectly confirmed the essential effect of island area, the significant increase in correlation strength when additional factors were implemented, clearly demonstrated their importance. Especially pronounced was the effect of habitat diversity (I), which increased the correlation strengths for species richness as well as for species composition in all studied archipelagos. These findings agree with empirical works which have shown either globally (Kreft et al. 2008, Hortal et al. 2009, Barajas-Barbosa et al. 2020) or in single archipelagos (Duarte et al. 2008 – Cape Verde, Roell et al. 2021 – Galápagos) that although island area is a crucial determinant of biodiversity, it does not fully override nor reflect the additional effect of habitat diversity on insular species richness.

Archipelago configuration affected species composition in elongated archipelagos, such as Hawaii and Azores, where circle randomization profoundly altered the overall connectivity of the archipelagos (I). However, archipelago spatial configuration did not affect species richness, which refers to the prevailing effect of other factors such as island area and habitat diversity, while species composition is more sensitive to the effect of archipelago configuration. This result agrees with a global study by Cabral et al (2014) who found island species richness as well as archipelago species richness to be strongly affected by the biogeography

and climate, whereas beta-diversity was mostly explained by the archipelago structure. The importance of archipelago structure both on island diversity and endemism has been also demonstrated in hypothetical archipelagos by Gascuel et al. (2016) with a spatially explicit neutral simulation model and by Aguilée et al. (2021) with an individual-based model which accounted for the spatio-temporal dynamics of the archipelagos. In contrast, in Galápagos and Cape Verde, I did not detect any effect of configuration randomization. This can be attributed owing to the more compact archipelago configuration, combined with more complex geological development of the archipelago which have been shown to alter the dispersal patterns between the islands (Carvalho et al. 2015).

In paper **II**, I demonstrated that the modern biodiversity of Hawaii and Galápagos is not fully adjusted to their current geography. Simulation scenarios, which concerned geological history, significantly decreased overestimations of native and endemic species richness on the youngest islands of both archipelagos. These results imply that despite the effect of habitat loss on the oldest islands (Price 2004), time available for immigration and speciation is a limiting factor of biodiversity variation on the entire archipelago level in the relatively young archipelagos, such as Hawaii and Galápagos. In Hawaii, historical dynamics also reduced the underestimation of species richness on Maui, Moloka‘i and O‘ahu, confirming the importance of the higher historical connectivity between these islands (Price and Elliott-Fisk 2004). Similarly, archipelago ontogeny has been demonstrated to significantly increase performance of grid-based island biodiversity simulations by Chalmardrier et al. (2018) and by Cabral et al. (2019b). However, a recent simulation study by Santos Neves (2022) showed that ignoring geodynamics still gave reasonable simulation results for isolated oceanic archipelagos. Combining the results of papers **I** and **II**, it appears that stronger reflection of historical (temporal) dynamics in the modern archipelago (spatial) configuration is why I found latter to strongly affect modern biodiversity patterns in Hawaii (**I**). On the contrary, in Galápagos, the complex patterns of landmass developments have caused more derivations from stepping-stone pattern, such as back-colonization events (Carvalho et al. 2015) and therefore, meaningful spatio-temporal patterns were first emulated by implementing geological history in paper **II** (but not by modern archipelago configuration in paper **I**).

In Canary Islands, implementing geological history even decreased correlations. It was mostly caused by the increased overestimation of single-island endemism (and to lesser degree, also of species richness) for the oldest and most degraded islands because of their increased availability for immigration and speciation in relation to younger islands of the archipelago. Thus, in contrary to Hawaii and Galápagos, in an old and mainland-close archipelago such as Canary Islands, erosion and consequent extinctions have become a limiting process. Also Carvalho et al. (2015) showed that whereas dispersal patterns in Hawaii can be successfully described by a relatively simple stepping-stone network model, much more complex patterns are needed for Canary Islands and Azores. Implementing eustatic history improved simulation performance in all three archipelagos, although, in Canary Islands the effect was significant only on single-island

endemics and not on total species richness (II). This finding is in line with other works that have demonstrated that although total species richness might adjust to the area change relatively quickly, endemic biodiversity patterns can have long-lasting legacies of historical connections and island areas (Weigelt et al. 2016, Norder et al. 2019).

In paper III, I approached another aspect of connectivity: the properties of the suboptimal habitat around the habitat fragments. I asked, how well are the Estonian old-forest fragments functionally connected by the surrounding secondary forests for several passively or slowly dispersing functional groups. I found ground layer vegetation, epiphytes, EcM and pathogenetic fungi to show dependence on old-forest availability in the surrounding of old-forest habitats: the more the simulation scenario favored the oldest forests over the other age classes, the better was the fit between the simulation results and observed data. However, saprotrophs followed an opposite trend: the most realistic biodiversity patterns were obtained by not differentiating between the forest age classes at all. This contrast might be caused by the more generalist strategy of saprotrophs who take over the former open habitat at the beginning of the secondary forest formation, whereas over the course of forest succession, ectomycorrhizal fungi start providing them competition (Cairney and Meharg 2002).

Several possible mechanisms have been proposed to explain the higher species richness in older forests. Similarly to oceanic islands, time that forest has been available for immigration (in landscape ecology, often called ‘habitat continuity’) in combination with dispersal limitation can be important, if forest-specific species are not locally available (e.g. Randlane et al. 2017). However, the effect of habitat quality has been found to often prevail over the habitat continuity (Norden and Appelqvist 2001). Diverse old forest offers several microhabitats for different species, as well as buffers the hostile environmental conditions. In paper III, I compared the effects of establishment and survival processes and found biodiversity of ground layer vegetation, epiphytes and EcM fungi to be clearly dominated by the establishment limitation. This finding is in line with many empirical studies from Estonia and Northern Europe that have found the suitable substrata to be of crucial importance in the oldest forests for lichens, fungi, and bryophytes (Fenton and Bergeron 2008, Lõhmus and Lõhmus 2011, Runnel and Lõhmus 2017). Specifically, I found that strongest correlations were obtained by low establishment probability in the abundant 40–50-year-old forests which have probably resulted from the abandonment of small farms, fields, and grasslands in the 1970s. Interestingly, no clear pattern revealed for the 70–80-year-old forests (contrasting scenarios gave similar results), although the minimum forest age to receive and support specific old-growth biodiversity has been typically shown to be even higher in Estonia (~100 years, Lõhmus & Lõhmus 2011) as well as elsewhere in Europe (200 years, or at least two or three generations, Graae 2000, Fritz et al. 2008, Dittrich et al. 2013). Nevertheless, these results clearly indicate that for most functional groups, middle-aged forests, developed on former agricultural land, do not yet functionally connect the old forest patches.

My aim in this thesis was not to achieve real absolute species numbers but realistic biodiversity patterns among the islands and Estonian nemoral old-forest patches. In general, higher correlations were obtained in island studies (**I** and **II**), than for Estonian forests (**III**), which agrees with the well-established understanding of oceanic islands as relatively simple natural model systems (Vitousek 2002, Warren et al. 2015). As discussed above, among the archipelagos, Hawaii showed the highest correlations between the observed and simulated species richness and always gave expected results in the scenario comparisons, whereas the biotas of other archipelagos proved more complicated to emulate. For instance, in Canary Islands, proximity of the mainland, prevailing winds and currents, and repeated volcanic activity, which has ‘restarted’ species accumulation on the islands, may all have had a significant effect on biodiversity development. Several additional processes, acting on different ecological levels (such as trophic interactions, intraspecific variation, demographics, metabolic constraint, natural and anthropogenic disturbances) have been argued to be important to consider in models for obtaining realistic biogeographical or macroecological patterns (Cabral et al. 2017, 2019b, Leidinger and Cabral 2017, Hagen et al. 2021).

However, using correlation strength between simulated and empirical data as a dependent variable in statistical models assumes some variation in the correlation strength. Moreover, low correlations or unexpected scenario comparisons can be helpful in detecting data gaps or differences among the study objects. For example, in paper **II**, an unexpected decrease in correlation strength if geological history was implemented in Canary Islands, referred to the crucial role of habitat loss owing to erosion. In paper **III**, contrasting trend of saprotrophs and only negative correlations in woody plants, AM fungi and carabid beetles pointed at their different ecology and that their diversity patterns could be possibly emulated by a different simulation model. It might be attempting to parametrize a simulation model to the best achievable fit with the empirical data. However, because of the inevitable trade-off between the model universality and realism, the necessity of additional details should always be weighed carefully. A more complex model does not necessarily lead to more realistic results, but it does always add additional uncertainty (Cabral et al. 2017).

5. CONCLUSIONS

Based on the results presented in this study, I conclude that:

1. Relatively simple agent-based simulation models could largely emulate natural patterns on oceanic islands (**I** and **II**) and – although with somewhat smaller accuracy – in Estonian forest fragments (**III**). This simultaneously demonstrates the relative simplicity of the island biotas and their role as ecological model systems as well as the usefulness of agent-based models for biogeography and landscape ecology. Their spatially explicit and mechanistic nature, together with pattern-oriented approach offers an intuitive and well-controllable approach for large-scale virtual experiments that are not feasible in the real world. Thus, they are a powerful tool for understanding biodiversity patterns of both – real and habitat – islands, as well as for predicting and avoiding biodiversity losses in these systems.
2. Despite the strong island area effect, habitat diversity and archipelago configuration are significant drivers of biodiversity on oceanic islands. Habitat diversity had strong effect in all studied archipelagos and on species richness as well as on species composition (**I**). Archipelago configuration had significant effect only in elongated archipelagos and affected species composition but not species richness (**I**).
3. Modern biodiversity of oceanic archipelagos carries legacies of the geological and eustatic processes of the past. Archipelago history and consequent spatio-temporal connectivity had a slightly stronger effect on proportion of single-island endemics than on total species richness (**II**).
4. Young and middle-aged forests are not supporting functional connectivity among the Estonian nemoral old-forest fragments for several forest-specific functional groups, such as ground layer vegetation, epiphytes, EcM and pathogenic fungi, and this obstacle has a significant effect on their biodiversity in old-forest patches (**III**).
5. Establishment limitation dominates over survival limitation in young to middle-aged forests, suggesting that microhabitat availability is the most important mechanism behind the old-forest affinity. Especially significant proved to be the effect of the abundant 40–50-year-old secondary forests on former agricultural land. On the other hand, functional connectivity among the forest fragments is strongly group-specific: while for most studied groups forest fragments can be considered almost as islands, saprotrophic fungi can successfully exploit the younger forests as well.

REFERENCES

- Aguilée, R. et al. 2021. Biogeographic drivers of community assembly on oceanic islands: The importance of archipelago structure and history. – *J Biogeogr* 48: 2616–2628.
- Amante, C. and Eakins, B. W. 2009. ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis. – NOAA Technical Memorandum NESDIS NGDC-24
- Arechavaleta, M. et al. 2005. Lista preliminar de especies silvestres de Cabo Verde (hongos, plantas y animales terrestres). – Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias.
- Arechavaleta, M. et al. 2009. Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. – Gobierno de Canarias.
- Barajas-Barbosa, M. P. et al. 2020. Environmental heterogeneity dynamics drive plant diversity on oceanic islands. – *J Biogeogr* 47: 2248–2260.
- Bintanja, R. et al. 2005. Modelled atmospheric temperatures and global sea levels over the past million years. – *Nature* 437: 125–128.
- Borges, P. A. V. and Hortal, J. 2009. Time, area and isolation: factors driving the diversification of Azorean arthropods. – *J Biogeogr* 36: 178–191.
- Borregaard, M. K. et al. 2016. The general dynamic model: towards a unified theory of island biogeography? – *Global Ecology and Biogeography* 25: 805–816.
- Botkin, D. B. et al. 1972. Some Ecological Consequences of a Computer Model of Forest Growth. – *J Ecol* 60: 849–872.
- Boyer, A. G. 2008. Extinction patterns in the avifauna of the Hawaiian islands. – *Divers Distrib* 14: 509–517.
- Brown, J. H. and Kodric-Brown, A. 1977. Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. – *Ecology* 58: 445–449.
- Bush, M. B. and Whittaker, R. J. 1993. Non-Equilibration in Island Theory of Krakatau. – *J Biogeogr* 20: 453–457.
- Cabral, J. S. et al. 2014. Biogeographic, climatic and spatial drivers differentially affect α -, β - and γ -diversities on oceanic archipelagos. – *Proceedings of the Royal Society B: Biological Sciences* 281: 20133246.
- Cabral, J. S. et al. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. – *Ecography* 40: 267–280.
- Cabral, J. S. et al. 2019a. Assessing predicted isolation effects from the general dynamic model of island biogeography with an eco-evolutionary model for plants. – *J Biogeogr* 46: 1569–1581.
- Cabral, J. S. et al. 2019b. Interactions between ecological, evolutionary and environmental processes unveil complex dynamics of insular plant diversity. – *J Biogeogr* 46: 1582–1597.
- Cairney, J. W. G. and Meharg, A. A. 2002. Interactions between ectomycorrhizal fungi and soil saprotrophs: Implications for decomposition of organic matter in soils and degradation of organic pollutants in the rhizosphere. – *Canadian Journal of Botany* 80: 803–809.
- Cardoso, P. et al. 2010. Drivers of diversity in Macaronesian spiders and the role of species extinctions. – *J Biogeogr* 37: 1034–1046.
- Carvalho, J. C. et al. 2015. Modeling directional spatio-temporal processes in island biogeography. – *Ecol Evol* 5: 4671–4682.
- Chalmandrier, L. et al. 2018. Comparing spatial diversification and meta-population models in the indo-Australian Archipelago. – *R Soc Open Sci* 5: 171366.

- Cornell, H. V. and Harrison, S. P. 2014. What are species pools and when are they important? – *Annu Rev Ecol Evol Syst* 45: 45–67.
- Danielson, J. J. and Gesch, D. B. 2011. Global Multi-resolution Terrain Elevation Data 2010(GMTED2010). – U.S. Geological Survey Open-File Report 2011–1073
- DeAngelis, D. L. and Mooij, W. M. 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. – *Annu Rev Ecol Evol Syst* 36: 147–168.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. – *Biol Conserv* 7: 129–146.
- Dittrich, S. et al. 2013. Separating forest continuity from tree age effects on plant diversity in the ground and epiphyte vegetation of a Central European mountain spruce forest. – *Flora: Morphology, Distribution, Functional Ecology of Plants* 208: 238–246.
- Duarte, M. C. et al. 2008. Plant species richness in the Cape Verde Islands – eco-geographical determinants. – *Biodivers Conserv* 17: 453–466.
- Fenton, N. J. and Bergeron, Y. 2008. Does time or habitat make old-growth forests species rich? Bryophyte richness in boreal *Picea mariana* forests. – *Biol Conserv* 141: 1389–1399.
- Fernández-Palacios, J. M. and Whittaker, R. J. 2008. The Canaries: An important biogeographical meeting place. – *J Biogeogr* 35: 379–387.
- Fritz, Ö. et al. 2008. Does forest continuity matter in conservation? – A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. – *Biol Conserv* 141: 655–668.
- Funk, V. A. and Wagner, W. L. 1995. Biogeographic patterns in the Hawaiian Islands. – In: Wagner, W. L. and Funk, V. A. (eds), *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago*. Smithsonian Institution Press, pp. 379–419.
- Gascuel, F. et al. 2016. The effects of archipelago spatial structure on island diversity and endemism: predictions from a spatially-structured neutral model. – *Evolution (N Y)* 70: 2657–2666.
- Geist, D. J. et al. 2014. A paleogeographic model of the Galápagos Islands and biogeographic and evolutionary implications. – In: *The Galapagos: A Natural Laboratory for the Earth Sciences*, Geophysical Monograph 204. pp. 145–166.
- Gilpin, M. E. and Diamond, J. M. 1976. Calculation of immigration and extinction curves from the species-area-distance relation. – *Proc Natl Acad Sci U S A* 73: 4130–4134.
- Gotelli, N. J. et al. 2009. Patterns and causes of species richness: a general simulation model for macroecology. – *Ecol Lett* 12: 873–886.
- Graae, B. J. 2000. The Effect of Landscape Fragmentation and Forest Continuity on Forest Floor Species in Two Regions of Denmark. – *Journal of Vegetation Science* 11: 881–892.
- Grimm, V. et al. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. – *Science (1979)* 310: 987–991.
- Hagen, O. 2022. Coupling eco-evolutionary mechanisms with deep-time environmental dynamics to understand biodiversity patterns. – *Ecography* 2022: e06132.
- Hagen, O. et al. 2021. gen3sis: A general engine for eco-evolutionary simulations of the processes that shape Earth's biodiversity. – *PLoS Biol* 19: 1–31.
- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 396: 41–49.
- Hanski, I. 2001. Spatially realistic theory of metapopulation ecology. – *Naturwissenschaften* 88: 372–381.
- Hanski, I. and Simberloff, D. 1997. The Metapopulation Approach, Its History, Conceptual Domain, and Application to Conservation. – In: Hanski, I. and Gilpin, M. E. (eds), *Metapopulation Biology*. pp. 5–26.

- Heaney, L. R. 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. – *Global Ecology and Biogeography* 9: 59–74.
- Hortal, J. et al. 2009. Island species richness increases with habitat diversity. – *American Naturalist* 174: E205–17.
- Illera, J. C. et al. 2016. What are We Learning about Speciation and Extinction from the Canary Islands? – *Ardeola* 63: 15–33.
- Imada, C. 2012. Hawaiian Native and Naturalized Vascular Plants Checklist (December 2012 update) (C Imada, Ed.). – *Hawaiian Native and Naturalized Vascular Plants Checklist*
- Izquierdo, I. et al. 2004. Lista de especies silvestres de Canarias (hongos, plantas y animales terrestres). – *Consejería de Medio Ambiente y Ordenación Territorial, Gobierno de Canarias*.
- Jaramillo Díaz, P. and Guézou, A. 2013. CDF Checklist of Galapagos Vascular Plants – FCD Lista de especies de Plantas Vasculares de Galápagos (F Bungartz, H Herrera, P Jaramillo, N Tirado, G Jiménez-Uzcátegui, D Ruiz, A Guézou, and F Ziemmeck, Eds.). – *Charles Darwin Foundation / Fundación Charles Darwin*.
- Jiménez-Uzcátegui, G. et al. 2014. CDF Checklist of Galapagos Birds (F Bungartz, H Herrera, P Jaramillo, N Tirado, G Jiménez-Uzcátegui, D Ruiz, A Guézou, and F Ziemmeck, Eds.). – *Charles Darwin Foundation / Fundación Charles Darwin*.
- Kazmierczak, M. et al. 2016. Monodominance in tropical forests: modelling reveals emerging clusters and phase transitions. – *J R Soc Interface* 13: 20160123.
- Kreft, H. et al. 2008. Global diversity of island floras from a macroecological perspective. – *Ecol Lett* 11: 116–127.
- Kupfer, J. A. et al. 2006. Not seeing the ocean for the islands: The mediating influence of matrix-based processes on forest fragmentation effects. – *Global Ecology and Biogeography* 15: 8–20.
- Leidinger, L. and Cabral, J. S. 2017. Biodiversity dynamics on Islands: Explicitly accounting for causality in mechanistic models. – *Diversity (Basel)* 9: 30.
- Levins, R. 1969. Some Demographic and Genetic Consequences of Environmental Heterogeneity for Biological Control. – *Bulletin of the Entomological Society of America* 15: 237–240.
- Löhmus, A. and Löhmus, P. 2011. Old-forest species: The importance of specific substrata vs. stand continuity in the case of calicioid fungi. – *Silva Fennica* 45: 1015–1039.
- MacArthur, R. H. and Wilson, E. O. 1963. An Equilibrium Theory of Insular Zoogeography. – *Evolution (N Y)* 17: 373–387.
- Matthews, T. J. et al. 2020. The effect of species extinctions on island biogeographic patterns. – *Ecol Res* 35: 372–381.
- Metzger, A. M. J. et al. 2005. A Climatic Stratification of the Environment of Europe Linked references are available on JSTOR for this article : A climatic stratification of the environment of Europe. 14: 549–563.
- Nishida, G. M. 2002. Bishop Museum-Hawaiian Arthropod Checklist. – *Bishop Museum, The State Museum of Natural and Cultural History*.
- Nordén, B. and Appelqvist, T. 2001. Conceptual problems of ecological continuity and its bioindicators. – *Biodivers Conserv* 10: 779–791.
- Nordén, B. et al. 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. – *Ecoscience* 21: 34–45.

- Norder, S. J. et al. 2019. Beyond the Last Glacial Maximum: Island endemism is best explained by long-lasting archipelago configurations. – *Global Ecology and Biogeography* 28: 184–197.
- Noreika, N. et al. 2019. Forest biomass, soil and biodiversity relationships originate from biogeographic affinity and direct ecological effects. – *Oikos* 128: 1653–1665.
- Peck, S. B. 2017. CDF Checklist of Galapagos Beetles – FCD Lista de especies de Escarabajos Galápagos. (F Bungartz, H Herrera, P Jaramillo, N Tirado, G Jiménez-Uzcátegui, D Ruiz, A Guézou, and F Ziemmeck, Eds.). – Charles Darwin Foundation / Fundación Charles Darwin.
- Price, J. P. 2004. Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. – *J Biogeogr* 31: 487–500.
- Price, J. P. and Elliott-Fisk, D. 2004. Topographic history of the Maui Nui complex, Hawai'i, and its implications for biogeography. – *Pac Sci* 58: 27–45.
- R Core Team 2022. R: A Language and Environment for Statistical Computing.
- Randlane, T. et al. 2017. Diversity of lichens and bryophytes in hybrid aspen plantations in Estonia depends on landscape structure. – *Canadian Journal of Forest Research* 47: 1202–1214.
- Roell, Y. E. et al. 2021. Effect of topographic complexity on species richness in the Galápagos Islands. – *J Biogeogr* 48: 2645–2655.
- Rohwäder, M. S. and Jeltsch, F. 2022. Foraging personalities modify effects of habitat fragmentation on biodiversity. – *Oikos* 2022: e09056.
- Roque-Álbelo, L. and Landry, B. 2018. CDF Checklist of Galapagos Butterflies and Moths – FCD Lista de especies de Mariposas y polillas Galápagos. (F Bungartz, H Herrera, P Jaramillo, N Tirado, G Jiménez-Uzcátegui, D Ruiz, A Guézou, and F Ziemmeck, Eds.). – Charles Darwin Foundation / Fundación Charles Darwin.
- Rosenberg, D. K. et al. 1997. Biological corridors: Form, function, and efficacy. Linear conservation areas may function as biological corridors, but they may not mitigate against additional habitat loss. – *Bioscience* 47: 677–687.
- Rosindell, J. and Phillimore, A. B. 2011. A unified model of island biogeography sheds light on the zone of radiation. – *Ecol Lett* 14: 552–560.
- Rosindell, J. and Harmon, L. J. 2013. A unified model of species immigration, extinction and abundance on islands. – *J Biogeogr* 40: 1107–1118.
- Runnel, K. and Löhmus, A. 2017. Deadwood-rich managed forests provide insights into the old-forest association of wood-inhabiting fungi. – *Fungal Ecol* 27: 155–167.
- Santos Neves, P. et al. 2022. The robustness of a simple dynamic model of island biodiversity to geological and sea-level change. – *J Biogeogr* 49: 2091–2104.
- Schoener, T. W. 2010. The MacArthur-Wilson equilibrium model a chronicle of what it said and how it was tested. – In: Losos, J. B. and Ricklefs, R. E. (eds), *The Theory of Island Biogeography Revisited*. Princeton University Press, pp. 52–87.
- Silva, L. et al. 2005. List of vascular plants (Pteridophyta and Spermatophyta). – In: Borges, P. A. V. et al. (eds), *A list of the terrestrial fauna (Mollusca and Arthropoda) and flora (Bryophyta, Pteridophyta and Spermatophyta) from the Azores*. Direcção Regional do Ambiente and Universidade dos Açores, pp. 131–156.
- Taylor, P. D. et al. 1993. Connectivity Is a Vital Element of Landscape Structure. – *Oikos* 68: 571–573.
- Terborgh, J. 1975. Faunal Equilibria and the Design of Wildlife Preserves. – In: *Tropical Ecological Systems*. pp. 369–380.
- Tischendorf, L. and Fahrig, L. 2000. On the usage and measurement of landscape connectivity. – *Oikos* 90: 7–19.

- Trapp, S. E. et al. 2019. Modeling impacts of landscape connectivity on dispersal movements of northern flying squirrels (*Glaucomys sabrinus griseifrons*). – *Ecol Modell* 394: 44–52.
- Travis, J. M. J. et al. 2005. The interplay of positive and negative species interactions across an environmental gradient: insights from an individual-based simulation model. – *Biol Lett* 1: 5–8.
- Valente, L. M. et al. 2015. Equilibrium and non-equilibrium dynamics simultaneously operate in the Galápagos islands. – *Ecol Lett* 18: 844–852.
- Vitousek, P. M. 2002. Oceanic islands as model systems for ecological studies. – *J Biogeogr* 29: 573–582.
- Warren, B. H. et al. 2015. Islands as model systems in ecology and evolution: Prospects fifty years after MacArthur-Wilson. – *Ecol Lett* 18: 200–217.
- Weigelt, P. and Kreft, H. 2013. Quantifying island isolation – insights from global patterns of insular plant species richness. – *Ecography* 36: 417–429.
- Weigelt, P. et al. 2016. Late Quaternary climate change shapes island biodiversity. – *Nature* 532: 99–102.
- Weigelt, P. et al. 2020. GIFT – A Global Inventory of Floras and Traits for macroecology and biogeography. – *J Biogeogr* 47: 16–43.
- Whittaker, R. J. and Fernández-Palacios, J. M. 2007. *Island Biogeography: Ecology, Evolution, and Conservation*. – Oxford University Press.
- Whittaker, R. J. et al. 2008. A general dynamic theory of oceanic island biogeography. – *J Biogeogr* 35: 977–994.
- Willerslev, E. et al. 2002. Number of endemic and native plant species in the Galápagos Archipelago in relation to geographical parameters. – *Ecography* 25: 109–119.
- Wilson, J. T. 1963. A Possible Origin of the Hawaiian Islands. – *Can J Phys* 41: 863–870.
- Xiao, S. et al. 2010. The effects of species pool, dispersal and competition on the diversity-productivity relationship. – *Global Ecology and Biogeography* 19: 343–351.
- Zeller, K. A. et al. 2020. Forecasting seasonal habitat connectivity in a developing landscape. – *Land (Basel)* 9: 233.
- Zobel, M. 2016. The species pool concept as a framework for studying patterns of plant diversity. – *Journal of Vegetation Science* 27: 8–18.

SUMMARY

Oceanic islands and habitat fragments within landscapes are both valuable ecological study objects, characterized by clear physical boundaries, immigration and extinction dynamics of well-defined populations, and high conservation priority. Therefore, the most influential model of island studies – theory of island biogeography – was historically also adopted to study the fragmented landscapes. Similarly, when later metapopulation theory gained popularity among landscape ecologist, it also inspired island biogeographers. Both theories emphasize the importance of spatial arrangement of individuals and populations and resulting ecological interactions and have been even called different aspects of a same theory. Classically, island biogeography and landscape ecology have been dominated by correlational methods and thus often mechanisms behind the biodiversity patterns have stayed unsettled. For example, the effects of island habitat diversity, archipelago configuration and island history on its biodiversity are hard to disentangle from the well-established effects of island area and isolation. Similarly, the mechanisms behind the forest connectivity and old-forest affinity of forest-specific biota are unclear.

In this thesis, I mechanistically explored the biodiversity drivers in oceanic archipelagos (Hawaii, Galápagos, Canary Islands, Cape Verde, Azores) and Estonian old-forest fragments, that are both characterized by spatial and functional isolation. I used spatially explicit agent-based simulation models together with empirical biodiversity data and compared different simulation scenarios in their ability to emulate realistic biodiversity patterns. In paper **I**, I showed that despite the substantial effect of island area, implementing habitat diversity in simulations always increased correlations between the simulated and observed plant species richness and composition, demonstrating the additional effect of varying environments. Implementing realistic archipelago configuration instead of randomizations proved to be important for gaining more realistic species composition patterns in elongated archipelagos, such as Hawaii and Azores, but did not affect species richness. This result again indirectly refers to the crucial role of island area for species richness development, whereas species composition is more sensitive to additional drivers. In Galápagos and Cape Verde, I did not find any effect of using real modern archipelago configuration, which hinted at the over-riding role of more complex spatio-temporal development of these archipelagos. This hypothesis was also supported by the results of paper **II**, where simulation scenarios which accounted for the geological and eustatic archipelago history, resulted in significantly more realistic results on the native and endemic species richness of birds, plants and insects of Hawaii and Galápagos, than the scenarios using static present-day maps. In Canary Islands, implementing eustatic history significantly increased the correlations but geological history had no positive effect, which referred to the importance of other processes, such as habitat degradation or repeated volcanic activity in this very old archipelago.

In paper **III**, I approached another aspect of connectivity: the properties of the suboptimal habitat around the Estonian nemoral old-forest fragments. Despite the apparent similarity, there is a crucial difference between oceanic islands and habitat fragments. Unlike real islands, isolation of habitat patches is not solely affected by their spatial arrangement, but also by organisms' response to the surrounding landscape, or the 'functional connectivity'. Estonian old-forest fragments are surrounded by non-forest and anthropogenic habitats, but also by younger secondary forests on former agricultural land. Whereas grasslands or anthropogenic landscapes might be totally uninhabitable for old-forest specific biodiversity, these secondary forests could be inhabitable to some degree. Therefore, I asked, how well are the Estonian old-forest fragments functionally connected by the surrounding younger forests for passively or slowly dispersing organisms. I found for ground layer vegetation, epiphytes, EcM and pathogenetic fungi, that the more the simulation scenario favored the oldest forests over the other age classes in terms of establishment and survival probabilities, the more realistic were the simulation results. This clearly indicates that for most functional groups, secondary forests on former agricultural land do not functionally connect the old-forest fragments. In contrast, the most realistic biodiversity patterns on saprotrophs were obtained by not differentiating between the forest age classes at all, hinting that for this group, forest connectivity is not limited by the age of the forest in the surrounding landscape. I also compared the effects of establishment and survival processes and found biodiversity of ground layer vegetation, epiphytes and EcM fungi to be clearly dominated by the establishment limitation, confirming the understanding of old-forest affinity being mainly caused by microhabitat limitation.

In conclusion, biodiversity in oceanic archipelagos and habitat fragments develops as a result of many interacting factors, which are often hard to disentangle in the nature. Spatially explicit and intuitively parametrizable agent-based models allow us to create virtual experiments for gaining mechanistic knowledge which is crucial for predicting and avoiding biodiversity losses in these isolated and valuable systems.

SUMMARY IN ESTONIAN

Elurikkust kujundavad tegurid ookeanisaarestikes ja killustunud elupaikades uurituna agendipõhiste mudelitega

Saari peetakse ideaalseteks ökoloogilisteks mudelsüsteemideks nende selgete füüsiliste piiride ja defineeritavate populatsioonide tõttu. Samuti on sajandeid teadlaste tähelepanu köitnud saarte eripärane ja kergesti haavatav elustik ning kõrge endeemsete liikide osakaal. Ookeanisaared, mis pole kunagi mandriga ühenduses olnud, sobivad uurimaks, kuidas elurikkus kujuneb sisserände ja evolutsiooni koosmõjul. Peale selle toimivad ookeanisaarestikud huvitavate võrgustikena, kus saarte paiknemine üksteise suhtes mõjutab liikide levimist. Sarnased võrgustikud on inimtegevuse tagajärjel tekkinud killustunud elupaigad, seda nii looduskaitse olulisuse pärast kui ka selle poolest, et pakuvad võimalust uurida rohkem või vähem isoleeritud populatsioonide dünaamikat. Seetõttu on ookeanisaarte ja killustunud koosluste uurimine aastakümneid arenenud käsi-käes.

R. MacArthuri ja E. O. Wilsoni poolt 1963. aastal avaldatud saarte biogeograafia tasakaaluteooria pani aluse nii saarte kui ka elupaigalaikude liigirikkuse dünaamilisele käsitlemisele. Teooria põhiidee järgi suurendab saare väiksem isoleeritus tõenäosust liikide sisserändeks, samal ajal kui liikide väljasuremise tõenäosus on väiksem suuremal saarel. Kahe protsessi vahel tekib dünaamiline tasakaal, mis hoiab liikide arvu saarel enam-vähem muutumatuna, kuna mõlemad protsessid sõltuvad ka saarel juba olemasolevate liikide arvust. Hiljem on sellele teooriale küll ette heidetud mitmete tegurite (nagu elupaikade mitmekesisus saarel, geoloogiline ajalugu ja saarte paiknemine saarestikena) arvestamata jätmist, kuid siiski sai sellest aastakümneteks paradigma, mida rakendati ka maastikuökoloogias killustunud elupaigalaikude uurimisel. 1980ndate aastate lõpus hakkas aga maastikuökoloogias populaarsust koguma kontseptuaalselt lähedane metapopulatsiooniteooria, mis tegeleb ruumiliselt eraldatud, kuid levivate isendite kaudu ühenduses olevate osapopulatsioonidega. Sarnaselt saarte biogeograafia teooriale on metapopulatsiooniteooria tuumaks isendite ja populatsioonide ruumiline paigutus ja sellest tulenevad ökoloogilised interaktsioonid, mistõttu on neid kahte teooriat nimetatud ka ühe üldisema teooria teisenditeks.

Kuigi saari ja killustunud elupaiku on ajalooliselt käsitletud sarnastena, on nende vahel siiski üks oluline erinevus: erinevalt saartest ei määra elupaigalaikude isolatsiooni ainult nende ruumiline paigutus, vaid ka levivate organismide võimekus ümbritsevas maastikus toime tulla. Näiteks Eesti vanu laialehiseid metsatukkasid ümbritsevate elupaikade hulgas on nii selliseid, mis on metsaelustikule täiesti sobimatud, kui ka selliseid, mis võivad vanametsa-spetsiifilist elustikku teatud määral toetada. Funktsionaalne sidusus iseloomustab, kui hästi organismid on võimelised elupaigalaikude vahel liikuma ning aeglaselt või passiivselt levivate organismide puhul võib oluline olla ka see, kui hästi nad suudavad seda maastikku ajutiselt asustada. Sarnaselt saartega soodustab elupaiga-

laikude suur sidusus (väike isolatsioon) sisserännet ja kõrgemat liigirikkust. Samuti on teada, et vanemad metsad toetavad kõrgemat liigirikkust, kuid ei ole selge, kuidas ümbritseva metsa vanus mõjutab vanametsalaikude funktsionaalset sidusust.

Saarte biogeograafias on klassikaliselt valitsenud korrelatiivsed meetodid, mille peamiseks puudujäägiks peetakse vähest võimet selgitada välja põhjuslikke seoseid. Seetõttu on informatiivsema meetodina välja pakutud protsessipõhised mudelid, mis simuleerivad põhjuslikke seoseid protsesside ja elurikkuse mustrite vahel. Agendipõhised mudelid toimivad reeglite kaudu, mis kehtivad iseseisvatele agentidele, kelleks võivad olla üksikud isendid või sarnaste isendite grupid. Kõrgema tasandi mustrid tekivad sel juhul „alt üles“. Oluliselt rohkem kui saarte biogeograafias on agendipõhiseid simulatsioone kasutatud maastikuökoloogias ning ka metsade sidususe uurimiseks, kuid need on peamiselt käsitlenud loomade käitumist ja rännet. Oma protsessipõhise ja ruumiliselt täpse olemuse, stohhastilisuse ja võrdlemisi napi parametrizeerimise tõttu võivad agendipõhised simulatsioonid olla aga kasulikud nii passiivse levimise uurimiseks maastikuökoloogias kui ka saarte biogeograafia jaoks.

Oma doktoritöös uurisin agendipõhiste simulatsioonimudelitega elurikkust kujundavaid tegureid ruumiliselt ja funktsionaalselt isoleeritud süsteemides: ookeanisaarestikes ja elupaigalaikudes. Tahtsin teada, kui hästi suudab võrdlemisi lihtne simulatsioonimudel jäljendada elurikkuse mustreid ookeanisaarestikes ja elupaigalaikudes; kas elupaikade mitmekesisusel ja saarestiku konfiguratsioonil on elurikkuse kujunemisel roll lisaks saare pindala tugevale efektile; kas tänapäevastes elurikkuse mustrites kajastub saarestike ajalugu; kuivõrd on Eesti laialehised vanad metsad funktsionaalselt ühendatud nooremate sekundaarsete metsade abil ning mis protsess sidusust enim mõjutab.

Kasutatud protsessipõhine, stohhastiline ja ruumiliselt täpne mudel simuleeris virtuaalsete taksonite alampopulatsioonide dünaamikat ookeanisaarte vahel saarestikes ning 5 km raadiuses vanametsalaikude ümber. Simulatsioonides kasutasin Hawaii saarte, Galápagose saarte, Kanaari saarte, Roheneemesaarte ja Assooride ning Eesti laialehiste metsalaikude rasterkaarte. Simulatsiooni agentideks olid virtuaalse taksoni alampopulatsioonid, mis teatud tõenäosusega immigreerusid uuritavale alale, asustasid vabu rastriruute, levisid, paljunesid, surid, ning – saarte simulatsioonide puhul – ka evolutsioneerusid. Kasutades nn muustrile orienteeritud lähenemist, võrdlesin erinevate simulatsioonistsenaariumite elurikkuse mustreid empiiriliste elurikkuse andmetega, leidmaks, millised parameetrite kombinatsioonid loovad tegelikkusega paremini vastavuses olevaid tulemusi. Artiklis **I** võrdlesin maapinna kõrgusandmete põhjal elupaikadeks jagatud saartega stsenaariumeid sellistega, kus saartel puudusid erinevad elupaigad, ning tegelikkusele vastava saarestiku konfiguratsiooniga stsenaariumeid juhusliku saarte paigutusega stsenaariumitega. Artiklis **II** võrdlesin staatilisi saarestikumudeleid sellistega, kus saared muutusid ajas vastavalt nende geoloogilisele arengule ning globaalsele merevee taseme kõikumisele. Artiklis **III** võrdlesin omavahel stsenaariumeid, mis määratlesid erinevad asustamis- ja ellujäämistõenäosused (mis koos peegeldasid funktsionaalset sidusust) erivanuselistele metsadele vanade metsade lähimbruses. Artiklis **I** kasutasin ookeanisaarestike seemne- ja eostaimede andmeid,

artiklis **II** lisasin nendele rühmadele ka värvulised, mardikad ja liblikad. Artiklis **III** kasutasin Eesti metsade rohurinde, epifüütide, puittaimede, jooksiklaste ning ektomükoriisete, arbuskulaar-mükoriisete, patogeensete ja saprotroofsete seente andmeid.

Minu töö tulemused näitasid, et nii tänapäevane elupaikade mitmekesisus saarel ja saarestiku konfiguratsioon kui ka saarestiku geoloogiline ajalugu ning maailmameere taseme muutused pleistotseenis on mänginud olulist rolli ookeanisaarte elurikkuse kujunemisel. Artiklis **I** osutus elupaikade mitmekesisus saarel oluliseks teguriks realistlikumate simulatsioonitulemuste saamiseks kõigis uuritud saarestikes, seda nii seemne- kui ka eostaimede liigirikkuse ja liigilise koosseisu puhul. See näitas, et hoolimata saare pindala tugevast mõjust on elupaikade mitmekesisusel elurikkusele täiendav efekt. Saarte paigutuse juhuslikustamine saarestikus ei mõjutanud simuleeritud liigirikkuse vastavust tegelikkusele, küll aga oli oluline mõlema taimerühma liigilise koosseisu jäljendamisel. See viitas taas saare pindala olulisele efektile liigirikkuse kujunemisel, samal ajal kui liigiline koosseis on kergemini mõjutatav lisateguritest. Saarte realistlik paigutus saarestikus oli siiski oluline vaid pikliku kujuga saarestikes nagu Hawaii ja Assoorid, osutades, et teistes saarestikes on saartevahelisi levimismustreid mõjutanud keerulisemad ajalis-ruumilised protsessid, mistõttu ei seleta tänapäevane saarte paigutus oluliselt nende elurikkust. Ka artikkel **II** kinnitas seda hüpoteesi, näidates, et Hawaii ja Galápagose saarte tänapäevane liigirikkus ja endeemse elurikkuse osakaal taime- ja putukarühmades on mõjutatud saarte vanusest ning geoloogilise arengu ja veetaseme kõikumise põhjustatud kunagistest saarte suurustest ja omavahelistest ühendustest. Artiklite **I** ja **II** tulemuste kombineerimisel saab selgeks, et kui saarestiku ajalugu peegeldub hästi saarte tänapäevases paigutuses (nagu Hawaii puhul), siis seletab viimane saarte liigilist koosseisu; kui aga saarestiku ajaloo jooksul on toimunud saarestiku konfiguratsioonis suured muutused (nagu Galápagosel), ei ole tänapäeval saarte paigutusel olnud piisavalt aega elurikkusele mõju avaldada.

Kanaari saarestikus põhjustas geoloogilise ajaloo rakendamine mudelis aga hoopis tegelikkusega halvemas kooskõlas olevaid simulatsioonitulemusi. See tulenes peamiselt liigirikkuse tugevast ülehindamisest saarestiku vanimatel saartel, kus sisseränne ja evolutsioon said nooremate saartega võrreldes oluliselt kauem toimuda. Sellised tulemused viitasid, et erinevalt noortest saarestikest, nagu Hawaii ja Galápagos, ei piira vanas ja mandrilähedases Kanaari saarestikus saarte liigirikkust mitte sisserändeks ja liigitekkeks vajalik aeg, vaid oluline elupaikade kadu vanimatel erodeerunud saartel. Sarnaselt teiste saarestikega muutis maailmameere taseme kõikumiste jäljendamine siiski simulatsioonitulemusi realistlikumaks ka Kanaari saarestikus, kuigi mõjutas vaid liigilist koosseisu, mitte liigirikkust.

Eesti laialehiste vanametsalaikude kohta leidsin, et paljude organismide jaoks ei ole nad funktsionaalselt hästi ühendatud. Simulatsioonitulemused korreleerusid seda tugevamini rohurinde, epifüütide, ektomükoriisete ja patogeensete seente empiiriliste elurikkuse andmetega, mida suuremad olid simulatsioonistsenaariumis erinevused asustamis- ja ellujäämistõenäosustes erineva vanusega metsade vahel. Eriti oluliseks osutus tugevate korrelatsioonide saavutamiseks madal asustamis-

tõenäosus ohtrates 40–50-aastastes metsades, mis on kujunenud endistele põllumaadele väikeste maamajapidamiste mahajätmise tagajärjel 1970ndatel aastatel. Saprotroofsete seente puhul esines aga vastupidine trend: kõige realistlikumad olid simulatsioonitulemused, kui stsenaarium ei eristanud metsade vanuseklasse, mis näitab, et saprotroofsetele seentele ei ole metsa vanus maastikus oluline. Puittaimede, arbuskulaar-mükoriissete seente ja jooksiklaste empiirilised andmed andsid simulatsioonitulemustega ainult negatiivseid korrelatsioone, mis viitas, et nende elustikurühmade jaoks on noorem mets vanast metsast sobivam või eelistavad nad metsale üldse teisi elupaiku. Lisaks näitasid metsade simulatsioonide tulemused, et nooremate metsade kasutamist metsaspetsiifiliste gruppide poolt piirab rohkem nende asustamine kui seal ellujäämine. Sarnasele järeldusele on kaudselt jõutud ka varasemates töödes, mis on näidanud mikroelupaikade mitmekesisuse olulisust vanades metsades.

Kokkuvõtteks võib öelda, et elurikkus ookeanisaarestikes ja elupaigalaikudes kujuneb väga paljude protsesside koostoimel, mis teeb tihti põhjuslike seoste tuvastamise looduses keeruliseks. Võrdlemisi lihtsad agendipõhised mudelid võimaldavad aga teha suureskaalalisi virtuaalseid eksperimente ning koguda teadmisi põhjuslike suhete kohta, mis aitavad ennustada ja vältida elurikkuse kadusid neis väärtuslikes isoleeritud süsteemides.

ACKNOWLEDGEMENTS

My sincere gratitude goes to my supervisor, Meelis Pärtel, who has guided me throughout my entire academic training and introduced me to the fascinating fields of biogeography and ecological modeling. He has been a constant source of support, inspiration, and wisdom, which has enabled me to develop my own ideas and interests, yet to remain within the limits of professional research.

I am very grateful to the people of the Macroecology, Landscape Biodiversity and Plant Ecology (*sensu lato*) workgroups. They are fun, smart, and encouraging as colleagues and as friends – they have made it a pleasure to come to work. I am also very honored to have had the opportunity to visit the Biodiversity, Macroecology and Biogeography workgroup at the University of Göttingen and to work alongside Holger Kreft and his colleagues, who made me feel most welcome.

A special thank you goes to my sister Kadri and my colleagues and friends Riin, Kersti and Martin for reading parts of this thesis with thoroughness exceeding my abilities.

And finally, I thank Säde coffee shop for the countless cups of coffee and hours of desk time since 2015.

The research presented in this thesis was funded by the Estonian Ministry of Education and Research (IUT20-29), Estonian Research Council (PRG609), European Union through the European Regional Development Fund (Centre of Excellence EcolChange) and Estonian State Forest Management Centre (project ‘Smart biodiversity conservation in Estonian natural and managed forests’).

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Publications

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Jõks, M., Kreft, H., Weigelt, P., Pärtel, M. 2021. Legacy of archipelago history in modern island biodiversity – An agent-based simulation model. – *Global Ecology and Biogeography* 30: 247–261.
Jõks, M. and Pärtel, M. 2019. Plant diversity in Oceanic archipelagos: realistic patterns emulated by an agent-based computer simulation. – *Ecography* 42: 740–754.

Conference presentations

- Jöks, M.**, Kreft, H., Weigelt, P., Pärtel, M. 2019. Effects of current and historical geography on island biodiversity revealed by an agent-based computer simulation (*oral presentation*). 3rdInternational Island Biology Conference, Saint-Denis, La Reunion.
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- Jöks, M.** and Pärtel, M. 2016. Plant diversity on oceanic islands: A computer simulation (*poster presentation*). 2ndInternational Island Biology Conference, Angra do Heroísmo, Azores.

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- 2016 SA Archimedes, Kristjan Jaak Scholarship for study period abroad

ELULOOKIRJELDUS

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Haridustee

2015–2023 Tartu Ülikool, Botaanika ja ökoloogia, doktoriõpe
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2012–2014 Tartu Ülikool, Bioloogilise mitmekesisuse kaitse, magistrikraad
2008–2012 Tartu Ülikool, Ökoloogia ning elustiku kaitse, bakalaureusekraad
märts–juuli 2011 Vahetussemester Konstanzi Ülikoolis Saksamaal
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Töökogemus

2022–2023 Tartu Ülikool, ökoloogia ja maateaduste instituut, makroökoloogia nooremteadur
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2018–2020 Tartu Ülikool, ökoloogia ja maateaduste instituut, ökoloogia spetsialist
2012–2014 Keskkonnaamet, looduskaitsebioloog

Peamised uurimisvaldkonnad

Saarte biogeograafia, maastikuökoloogia, killustunud elupaikade sidusus, ökoloogiline modelleerimine.

Teadusartiklid

Jõks, M., Helm, A., Kasari-Toussaint, L., Kook, E., Lutter, R., Noreika, N., Oja, E., Öpik, M., Randlane, T., Reier, Ü., Riibak, K., Saag, A., Tullus, H., Tullus, T., Pärtel, M. 2023. A simulation model of functional habitat connectivity demonstrates the importance of species establishment in older forests. – *Ecological Modelling* 481: 110361.
Jõks, M., Kreft, H., Weigelt, P., Pärtel, M. 2021. Legacy of archipelago history in modern island biodiversity – An agent-based simulation model. – *Global Ecology and Biogeography* 30: 247–261.
Jõks, M. ja Pärtel, M. 2019. Plant diversity in Oceanic archipelagos: realistic patterns emulated by an agent-based computer simulation. – *Ecography* 42: 740–754.

Konverentsiettekanded

Jõks, M., Kreft, H., Weigelt, P., Pärtel, M. 2019. Effects of current and historical geography on island biodiversity revealed by an agent-based computer simulation (*suuline ettekanne*). 3. Rahvusvaheline Saarte Bioloogia Konverents, Saint-Denis, La Reunion.

Jõks, M. ja Pärtel, M. 2017. An individual-based computer simulation can emulate realistic plant diversity patterns in oceanic archipelagos (*posterettekanne*). Briti Ökoloogilise Ühingu (BES), GfÖ, NecoV ja Euroopa Ökoloogia Liidu (EEF) ühine aastakonverents, Gent, Belgia.

Jõks, M. ja Pärtel, M. 2016. Plant diversity on oceanic islands: a computer simulation (*posterettekanne*). 2. Rahvusvaheline Saarte Bioloogia Konverents, Angra do Heroísmo, Assoorid.

Stipendiumid

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