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# Differences in root architecture influence the persistence time of competing species in simulated plant communities

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# Abstract

### Aims

Although several studies have shown that species interactions can support coexistence of plant species, our understanding of the role of root traits and architecture in coexistence is limited, despite their key role in resource acquisition. Theory suggests two seemingly contrasting outcomes: (1) when species share similar traits, competitive exclusion is slowed and persistence is prolonged, or (2) when species differ greatly in their traits, niche separation reduces competition allowing longer persistence. Here, we ask: Does greater divergence in root architecture increase or decrease persistence time in simulated plant communities?

### Methods

We use a functional-structural plant model to simulate the development of annual plant communities over time. The plants belong to one of five species that differ in root architecture, resulting from simulations of evolution under varying levels of competition.

### Results

Our findings support both theoretical predictions, but through different mechanisms. Differences in root morphology increase persistence time, with the two most different species persisting indefinitely. This appears to result from a density-dependent effect that enables species to recover from low densities. In contrast, in communities composed of ecologically identical species, persistence time seems to be governed by neutral drift and increased with their population density and area size.

### Conclusions

The magnitude of differences in root morphology of interacting species drive their expected persistence time through distinct mechanisms.


# Introduction

Identifying the mechanisms for species coexistence has been a major goal in ecology (Götzenberger et al., 2012; McCann, 2000, 2000; Silvertown, 2004) and, has critical applications for managing species loss, invasion, and reintroduction (Evans et al., 2022; Hallett et al., 2023; Miatta et al., 2021; Shea, 1998). species differ in these traits, some may be better equipped to withstand stress. For example, plants can exhibit different root architectures to endure varying levels of drought (Poot et al., 2012). According to Levin (1970), this could lead to species displacing one another if they compete for the same resource, i.e., competitive exclusion. However, some communities have more species than this prediction would suggest (Brumit et al., 2021; Cowling et al., 1996). Interactions among individuals, shaped by differences in their traits, behaviours, and strategies, can play a crucial role in determining whether species are able to coexist. For these and other types of interactions, differences among species remain a key

component of coexistence (Chesson, 2000; Gause, 1934; Godoy et al., 2017, 2020; Macarthur and Levins, 1967).

Two perspectives predict a seemingly contrasting relationship between species differences and coexistence: niche theory (e.g. Vandermeer, 1972) and neutral theory (e.g. Hubbell, 2000; Rosindell et al., 2011). According to Chase and Leibold (2003), the ecological niche is the set of conditions under which the birth rate of a population is equal to or higher to its death rate, including the impact of other species on those conditions. Many studies have shown that species coexistence is possible when there is niche differentiation, for example in resource use, habitat preference, or timing of activity (Hough-Snee et al., 2015; Wulf, 2003; Silvertown et al., 2015). This theory suggests that species that are more dissimilar are less likely to competitively exclude one another and more likely to coexist (Chesson, 2000). In contrast, a community is considered neutral if its species are ecologically equivalent, meaning that the traits in which they differ do not affect fitness or demographic rates (Leibold and McPeek, 2006). In such communities, random variations in demographic rates, local extinction, and immigration can allow species to coexist (Purves and Turnbull, 2010; Vellend, 2014). This theory implies that the more similar species are, the more likely coexistence is to occur.

Relatively little research has focused on the role of below-ground trait differences in promoting coexistence, which play a crucial role in water- and nutrient-limited ecosystems (Kiær et al., 2013). There is considerable theoretical and empirical work linking competition for below-ground resources with diversity and coexistence (Cabal et al., 2024; Lamb et al., 2009). However, it remains unclear whether differences in root architecture alone can drive patterns of coexistence. Testing whether such root traits influence species coexistence using empirical measurements is challenging due to factors such as large plant size, low population density, long germination times (Wright, 2002), and the inherent difficulty of measuring roots (Downie et al., 2015; Freschet et al., 2021; Maqbool, 2022). Bartomeus and Godoy (2018) identified disentangling the effects of various interactions as a major challenge in empirical studies of coexistence. As a complementary approach, functional–structural plant models (FSPMs) can be valuable tools, as they explicitly consider the 3D structure of roots, and can be used to study the dynamic development of individuals considering biotic and abiotic interactions (de Vries, 2021; Godin and Sinoquet, 2004). This modelling approach should allow us to study quantitatively how differences in root architecture affect long-term species coexistence, and isolate their effect from other factors and processes.

Here, we focus on plant root architecture, which refers to the topological and geometrical characteristics of a root system and can be described with metrics such as fractal dimensions (Hodge et al., 2009). We simulated the long-term ecological dynamics of plant communities made up of two species that differ, to varying degrees, in their root architecture, to test whether greater differences in root morphology led to longer coexistence. Based on the niche and neutral theories, we hypothesised that persistence time will be longest when species are either very similar or very different in root morphology, and shortest at intermediate levels of difference.

# Methods

### Root Growth Model Overview

We used a FSPM previously developed to simulate plants competing for water to explore the evolutionary advantages of different root architectures in different conditions, the full details of the model are presented in Renton and Poot (2014), Renton et al. (2025), and Salinas et al., (2026). In the model, plants are represented by an above-ground biomass compartment without explicit shape that includes reproductive organs, and a root biomass component with an explicit 3D structure. Roots extract water from the soil, which is then converted into both above-ground and root biomass. This FSPM incorporates 14 root architecture parameters that control branching probability, branching angle and rotation angle, maximum root order, growth priority per root order, gravitropism, proportion of root to above-ground biomass allocation, root base length, and branching probability, to dynamically simulate root growth. By varying the values of these parameters, roots with contrasting shapes and size can be simulated (e.g. Fig. 1, and those presented in Renton et al. (2025)). In this context, each plant has a “genotype”, meaning a specific set of these 14 parameter values used to simulate its growth.

Figure 1: Examples of root morphology for the five species. The examples show plants after 150 days of growth in isolation

### Species

We build on previous research by Salinas et al. (2026), who combined the FSPM with an evolutionary algorithm to find root architectures that tend to optimize above-ground biomass (assuming it includes reproductive organs) under increasing levels of below-ground competition for water.  In that study, the authors simulated the evolution of populations of initially random genotypes under selection in one five scenarios of increasing competitive pressure. Here, we define species as a set of 15 genotypes that result from the same evolutionary scenario For this study, we use five annual species: $Sp_0$, $Sp_1$, $Sp_2$, $Sp_3$, and $Sp_4$, each previously selected using the evolutionary algorithm under intraspecific competition with 0, 1, 2, 3, or 4 neighbouring plants, respectively, this was the competitive environment in which the species evolved as described by Salinas et al. (2026). These species are not meant to represent taxonomically defined species, but a range of strategies ranging from $Sp_0$ having denser and more shallow root system, to $Sp_4$ with deeper and more sparse roots. The FSPM simulates root growth dynamically and stochastically, meaning that two plants of the same species will exhibit similar but not identical root systems due to small differences in genotype within species, changing variations in environment due to interactions with competing plants and other roots of the same plant, and stochastic variation in development.

To characterise the overall root morphology of each species and quantify the magnitude of differences in root morphology across species, we computed a mean root morphology vector for each species. We simulated 100 plants of each species grown without neighbours for 150 time steps. The mean root morphology vector was defined as the set of average values for six traits describing overall global root

morphology, calculated on the whole final simulated root systems (in contrast to the 14 root parameters mentioned above, which are local traits that determine how an individual plant grows at each step of its development). These six global root traits were: fractal dimension (Tatsumi et al., 1989), root biomass, maximum root depth, maximum horizontal distance, root length per unit biomass, number of branches per unit root length, and root density per occupied soil voxel (Table 1). The morphological difference between any two species was then calculated as the Euclidean distance between their standardised mean root morphology vectors.

**Community dynamics model**

The FSPM simulates the growth of plant roots under competition for water, and was adapted to simulate community dynamics.  Plants grow within a soil volume of 400 mm × 400 mm × 1200 mm depth, which is divided into 20 × 20 × 60 voxels, each measuring 20 × 20 × 20 $mm^3$. Each soil voxel can hold up to 10% of its volume in water. Soil dynamics include water diffusion, evaporation, resupply, and uptake by plant roots.

For this study, we extended the FSPM to represent the long-term ecological dynamics of communities of interacting annual plants with non-overlapping generations and limited seed dispersal. A long-term simulation consists of a number of within-year simulations, each representing a community of plants growing for 150 days under conditions of constant irrigation (Fig. 1A–B). Each within-year simulation uses the FSPM to simulate the growth and soil-water-mediated competitive interactions of the multiple individual plants in the community (Renton et al. 2025 and Salinas et al. (2026) for details). After 150 days, seed production and dispersal are calculated, all plants die, and then the next generation is initialised and simulated.

Within-year simulations are initialised each year with newly germinating plants consisting of a single root segment at the top of the soil and no initial above-ground biomass (Fig. 1A). The position of the plants is constrained to a grid (different to the array of soil voxels), defined by conceptually overlaying a 2D lattice composed of 10 × 10 cells, each measuring 40 × 40 mm on the soil surface, with the centres of these cells defining potential locations for new plants. At most one plant can occupy each cell. In the first year of a long-term simulation, the within-year simulation is initialised according to the experiment being conducted (see below). In subsequent years, the within-year simulation is initialised based on the results of the previous year's simulation, as follows. At the end of a year, each plant produces seeds based on its above-ground biomass. Assuming that above-ground biomass includes both leaf and seed biomass, a minimum of avobe-ground biomasss (*BaseAbvGBiomass* = 8g) is required to produce any seeds, with each seed requiring a fixed biomass cost (*CostPerSeed* = 4g) of above-ground biomass. The number of seeds produced by a plant (*Nseeds*) is thus calculated as:

$$Nseeds = floor\left(\frac{x - BaseAbvGBiomass}{CostPerSeed}\right)$$

The seeds produced by a plant are dispersed into the surrounding environment with specific probabilities: a given seed has a 10% chance of dispersing to each of the eight adjacent cells, and a 20% chance of remaining in the parent plant's own cell. At the start of the next year, the next generation is initialised from the seeds present in each cell. For each cell, one seed is randomly selected to establish a new plant, assuming that only one seed can successfully establish per cell and that all seeds have an equal probability of doing so. If there is only one seed in the cell then it established and if there are no seeds in a cell, then no plant establishes and the cell remains empty.

**Pairwise persistence time experiments**

We conducted simulation experiments of plant communities made up of two species with varying degrees of difference in root morphology, and measured persistence time, defined as the duration for which both species remain present or coexist in the community. This measure is sometimes referred to as co-occurrence, to distinguish the temporary presence of multiple species from long-term stable persistence (Leibold and McPeek, 2006). We then compared these results to those from simulations of neutral communities and single species populations. Here, we define neutral communities as consisting of two "species" with the same root morphology, i.e., the same genotypes but labelled separately. This allowed us to track them as distinct species while ensuring they were functionally identical although this definition of neutral species is not identical to that of Hubbell (2001). We also recorded population density as the proportion of cells occupied by each species in each year of the simulation. At the end of all simulations we computed the mean of density per species.

Experiments were initialised with communities consisting of 16 plants (8 plants per species) distributed at random across the 100 cells. We conducted 10 experiments, each representing a different pairwise combination of two species from the total of five. In addition, we performed 5 experiments using neutral communities and 5 experiments with single species populations (one of each for each of the five species). Each experiment was repeated 20 times and ran for up to 500 years or until one of the species went extinct. In cases where extinction occurred, we used an exact binomial test to assess whether the probability of one species outcompeting the other differed significantly from 0.5, using the *binom.test*() function in R (R Core Team, 2025).

We performed a smaller set of experiments to analyse the effect of simulated area size on persistence time for both a pair of neutral species and a pair of non-neutral species. These experiments were initialised and run in the same manner as described previously. However, instead of using a square grid with 10 cells per side, we tested grids with 8, 12, 15, 18, and 20 cells per side, with three repetitions for each configuration.

# Results

The root morphology metrics per species show a clear gradient with $Sp_0$ and $Sp_4$ in the extremes (Table 1). An example of a community of $Sp_0$:$Sp_4$ within a year is shown in Fig. 2. An animation of the spatial

distribution of species over years in one of the long-term ecological simulations is provided in the Supplementary material (S1).

Table 1. Summary of the seven root architecture metrics for all species. Values correspond to the mean ± standard deviation of a sample of 100 plants

| Species | Fractal dimension | Root Biomass (g) | Maximum depth (mm) | Maximum horizontal distance (mm) | Root length per root biomass ($mm\ g^{-1}$) | No. Branches per root length ($mm^{-1}$) | Root density per voxel ($g\ voxel^{-1}$) |
|---|---|---|---|---|---|---|---|
| $Sp_0$ | 1.67 ± 0.021 | 40.86 ± 3.58 | 136.79 ± 12.98 | 122.02 ± 5.63 | 490.99 ± 16.50 | 0.028 ± 0.002 | 0.099 ± 0.006 |
| $Sp_1$ | 1.62 ± 0.024 | 35.38 ± 2.61 | 151.77 ± 19.61 | 129.31 ± 13.20 | 456.18 ± 19.41 | 0.031 ± 0.005 | 0.084 ± 0.007 |
| $Sp_2$ | 1.57 ± 0.044 | 34.00 ± 3.74 | 172.51 ± 13.82 | 143.18 ± 13.49 | 405.86 ± 22.91 | 0.025 ± 0.008 | 0.076 ± 0.008 |
| $Sp_3$ | 1.50 ± 0.029 | 27.69 ± 3.01 | 183.67 ± 23.21 | 158.64 ± 13.09 | 382.3 ± 24.26 | 0.017 ± 0.005 | 0.066 ± 0.004 |
| $Sp_4$ | 1.41 ± 0.029 | 25.66 ± 3.07 | 263.57 ± 26.82 | 184.45 ± 29.97 | 345.79 ± 17.47 | 0.01 ± 0.001 | 0.070 ± 0.006 |

Figure 2: Example of a community at the beginning (A) and at time-step 75 (B) of a simulation. The soil is represented as a set of cubic voxels (outline indicated by gray lines). Seeds (dots color coded according to the species) are placed in the centre of cells of a square grid (black lines). At the beginning of simulations, plants have a single root segment and no biomass. As plants gather water from the soil, they grow their roots (coloured lines, red for $Sp_0$ and blue for $Sp_4$) in space according to their genotype. Wrapping in the x and y dimension causes roots to appear disjointed.

**Population density**

The population density of each species within mixed-species communities differed from that observed in monocultures (Fig. 3 and 4). In monocultures, population density (proportion of cells occupied by a species) fluctuated around a mean value without a clear pattern (Fig. 3A). In contrast, species densities in mixed communities exhibited more cyclical oscillations and appeared to be negatively correlated with one another (Fig. 3B). The mean density differed among species and communities (Fig. 4). In monocultures, the average proportion of cells occupied by plants over time varied by according to the number of neighbours a species evolved alongside with. $Sp_0$, which evolved without neighbours, had the lowest density (0.24 on average). Density increased up to that of $Sp_4$ reaching the highest rate at 0.4

(Fig. 4). In the case of mixed communities, the proportional density (density per total cells per species) differed to that of monocultures (Fig. S1).

Figure 3: Population density per species across generations in three simulation experiments. Population density is the mean number of plants per cell, or (given that each cell can only hold one plant) the proportion of cells occupied by a plant Colours indicate each species; solid lines indicate population density and dashed lines indicate mean population density for the duration of the experiment. The experiments where initialised with the same density per species and included (A) monoculture of Sp4, (B) $Sp_0$:$Sp_4$ , and (C) $Sp_2$:$Sp_4$

Figure 4: Mean population density for the total duration of the experiments. The density corresponds to that of the species name indicated in the grid row name (underlined) in a community including the species indicated by the column name. The diagonal corresponds to the density of a mono-species or neutral community (which are the same as they are functionally identical). The mean was computed for 20 experiment repetitions.

**Persistence time**

Persistence time varied across species pairings, differing in both the mean (Fig. 5) and range (Fig. 6). Persistence times ranged from an average of 51.1 years for the $Sp_2$:$Sp_4$ combination to 500 years for $Sp_0$:$Sp_4$, indicating that Sp0:$Sp_4$ coexisted for the full duration of all 20 simulation replicates. Further experimentation showed that these two species can coexist for beyond 5000 years. In general, species pairs coexisted longer if the two species evolved under more contrasting competitive conditions (Fig. 5). Similarly, expected persistence time tended to increase with the difference in mean root morphology between the two species with a significant positive slope in a lineal model (Fig. 6). Among neutral communities, with two functionally identical species, mean persistence time was generally higher when using species evolved with more neighbours and with higher population densities (Fig. 4 and 5). $Sp_0$:$Sp_0$ had the shortest persistence time, while Sp3:Sp3 had the longest, although its distribution overlapped notably with that of $Sp_4$:$Sp_4$ (Fig. 6). The persistence time of neutral communities of $Sp_3$ and $Sp_4$ was longer than that of those species competing with each other or with $Sp_2$. Persistence time did not significantly change with the size of the grid for $Sp_3$:$Sp_4$, but it significantly increased in the neutral community $Sp_4$:$Sp_4$, being longer than 500 generations in two simulations (Fig 7).

Figure 5: Mean persistence time of communities per species pairing over 20 repetitions. The diagonal corresponds to the coexistence of neutral communities

Figure 6: Community persistence time as related to contrast in species' root morphology. Contrasts in mean root morphology are shown as the Euclidean distance in the standardised mean root morphology between a pair of species (see text). Persistence time is the number of generations until one species in the community goes extinct. Circles indicate the mean persistence time over 20 replicates and the bar the standard error. The colours of the circles show the two species that comprised the community,

single-coloured circles indicate neutral species communities (see text). Neutral communities all had a distance in mean root morphology of 0, but the position on the x-axis is shown jittered for visibility. The species on the left half (colour) was the one that survived more frequently; circles with a black outline indicate that this species was significantly more likely to persist while the other went extinct. The dashed line indicates the expected persistence time according to a linear model with an estimated slope of 61.58 (p=0.001)

Figure 7: Community persistence per grid size for a pair of neutral and non-neutral species. Persistence time is the number of generations until one species in the community becomes extinct. The communities develop in a square grid area composed of 8, 12, 15, 18, or 20 cells per side indicated in x axis. Each point represents an individual simulation; circles correspond to the pair $Sp_3$:$Sp_4$ and diamonds to the pair $Sp_4$:$Sp_4$. The lines indicate the expected persistence time per number of cells per side according to a linear model, with the solid line corresponding to $Sp_3$:$Sp_4$ and the dashed line to $Sp_4$:$Sp_4$.

# Discussion

Our results support the hypothesis that differences in root morphology can facilitate species coexistence, with greater differences in root architecture leading to longer mean persistence times, potentially even indefinitely. Additionally, our findings provide some support for the prediction that neutral communities, characterised by a lack of ecological differences among species, can also promote persistence, although to a smaller extent. This general pattern is consistent to the predictions of neutral, niche theories, and trait hierarchy (Mayfield and Levine, 2010). Persistence time (Fig. 5), mean population density (Fig. 4), and temporal variation in density (Fig. 3) all varied across different community compositions. Since all species shared identical physiology, seed cost, dispersal ability, and germination probability, the observed patterns can be attributed to biotic interactions mediated by differences in root architecture. These findings raise important questions about the mechanisms underlying long-term persistence which are discussed in the following paragraphs: why do only some species pairs persist indefinitely?; why does persistence time vary with the degree of species' difference?; and is competitive exclusion responsible for species extinction?

Only one of the communities persisted indefinitely ($Sp_0$:$Sp_4$), supporting the idea that root architecture differences can enable long-term coexistence. The five species differed in their root morphology along a continuum, with $Sp_0$ and $Sp_4$ representing the extremes (Salinas et al., 2026). $Sp_0$ has denser, shallower roots, while $Sp_4$ has sparser roots that grow deeper (Fig. 1, Table 1). This suggests that indefinite persistence is possible due to niche separation, where species exploit different soil zones through distinct root morphologies. This pattern aligns with empirical findings. For instance, Martínez-Blancas and Martorell (2020) documented coexistence among six annual species in southern Mexico based on differences in stress tolerance and root depth, while Cabal et al., (2024) found evidence of root biomass segregation per depth in three species of coexisting shrubs in in a Mediterranean shrubland in central Spain. The niche separation observed in our study appears more complex than simple spatial

partitioning. $Sp_4$, with its less dense and deeper roots, exhibits the lowest growth potential (measured as above-ground biomass in isolation which includes reproductive organs), suggesting it would be a weaker competitor and likely to be excluded. However, $Sp_4$ has the highest competitive resistance (above-ground biomass under competition), while $Sp_0$ the lowest (Salinas et al., 2026). This is consistent with the definition of a niche by Chase and Leibold (2003), which emphasises not only the conditions under which a species can persist but also how it modifies those conditions. Thus, only $Sp_0$ and $Sp_4$ persist indefinitely because their contrasting performance under high and low competition created a balance that prevented displacement. This is also consistent with Chesson (2000) who states that two species can coexist when negative intraspecific interactions are stronger than interspecific interactions.

Mean persistence time tended to increase with differences in root morphology (Fig. 5), and non-random competitive exclusion where one species consistently displaced the other was observed at intermediate levels of difference (indicated by solid outlines in circles in Fig. 6). These results suggest that as species differences increase, extinction takes longer and is less likely to occur. This pattern can be attributed to niche differences and the strength of density-dependent effects, which influence the likelihood of recovery from low population densities. Low levels of morphological difference (e.g., $Sp_1$:$Sp_2$) allow the stronger competitor to rapidly displace the weaker one. At intermediate levels of morphological difference (e.g., $Sp_1$:$Sp_3$), density dependence is not strong enough to maintain persistence indefinitely, nor are the trait differences large enough to drive rapid exclusion, making stochasticity a dominant factor, as reflected in the greater variability in persistence time and non-significant difference in probability of displacement. At high levels of difference (e.g., $Sp_0$:$Sp_4$), density-dependent effects are strong enough to prevent extinction, enabling indefinite persistence. This is consistent with Dybzinski and Tilman (2007), who observed that displacement rates among species slowed as differences in root depth and nitrogen use increased. Our results suggest that morphological differences that are not large enough to sustain species persistence indefinitely could be ecologically relevant, as the increased persistence time when combined with other constant mechanisms such as pathogen effects or herbivory, could cause long-term persistence. For example, Liu et al. (2022) found that removing foliar pathogens over three years reduced species richness in plant communities composed of 25 perennial species from Poaceae, Asteraceae, and Ranunculaceae on the Qinghai-Tibetan Plateau.

Notably, the $Sp_2$:$Sp_4$ community deviates from the overall trends observed in our results. Despite exhibiting a level of morphological difference comparable to $Sp_0$:$Sp_2$ this community showed a lower-than-expected persistence time. An explanation for this outlier could include a combination of (1) the set of morphological traits used to summarise morphology may fail to capture a biologically meaningful aspect of root behaviour (e.g. temporal patterns of growth); (2) root morphology measured in isolation may differ significantly from that expressed under competitive conditions; (3) Some species pairings have a stronger antagonistic effect. The inherently plastic nature of plant morphology results in root morphologies that differ across neighbour number, species and position which complicates efforts to quantify dissimilarities between species. Nevertheless, the resulting patterns indicate that the metrics of

morphological differences we use was adequate. Future research could include metrics that consider changes in morphology over time.

Neutral communities did not persist indefinitely. In these communities, each species was equally likely to go extinct, indicating that extinction was not driven by competitive exclusion but rather by random drift, consistent with a random walk (Aarssen, 1989; Purves and Turnbull, 2010). This is further supported by the increase in persistence time with area for neutral species, but not for the non-neutral pair. Interestingly, persistence time in neutral communities varied across species. Since extinction was driven by stochastic processes, species with higher population densities tended to persist longer (Fig. 4 and Fig. 6). Notably, our results show that neutral communities coexisted for longer than two species communities with low levels of morphological difference. For example, the Sp2:Sp3 community had a shorter persistence time than the Sp3:Sp3 neutral community (Fig. 6). This suggests that complete niche overlap, as in neutral communities, may allow for longer persistence than partial niche overlap, where even small differences can lead to faster competitive exclusion. In such cases, deterministic interactions may accelerate extinction more than random drift would.

The change in population density between a species grown in a monoculture vs in a community shows the species-specific effect of competition. If the two species did not interact at all and were confined to half of the space available, an adjusted density, considering the number of cells available per species, should be the same of monocultures. However, the results show that this adjusted density is not the same, indicating that one species is occupying a disproportionate amount of the space (Fig. S1). For example, $Sp_3$ and $Sp_4$ have mean densities in monocultures of 37/100 and 40/100. If the two species did not interact, they would be found in the same proportion but in a lower densities of 18.5/50 and 20/50 respectively. However, they were found to have densities of 0.29 and 0.08 (Fig. 4), $Sp_3$ occupying a disproportionate part of the space, and with $Sp_4$ eventually going extinct.

Our findings indicate that differences in root architecture influence persistence time, competitive exclusion, and population density. These effects arise from trade-offs mediated by root architecture. Similar trade-offs in strategies mediating coexistence have been proposed through game-theoretic analyses, including height-support costs, height-related mortality, and radiation absorption–water use efficiency (Falster and Westoby, 2003). Competitive exclusion did not occur at very low or very high levels of root morphological difference, and persistence time depended on species-specific root traits. Although the strategies we studied varied along a single gradient related to competitive ability, similar patterns might emerge when considering trait differences shaped by other selective pressures, such as spatial heterogeneity. However, this remains to be tested. It also remains an open question how important these root architecture differences are relative to shoot architecture differences or other coexistence mechanisms, such as seed dispersal or pathogen pressure, or interactions across more than two species. In such cases, neutral communities might persist even longer, suggesting that multiple mechanisms may interact to shape long-term persistence dynamics.

# Declarations

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**Competing Interests**

The authors declare no conflicts of interest.

**Author contributions**

Conceptualization HS MR, Data Curation HS, Formal Analysis HS MR, Funding Acquisition MR, Investigation HS MR ET EV, Methodology HS MR ET EV, Project Administration HS MR, Resources MR, Software HS MR, Supervision MR, Visualization HS, Writing – Original Draft HS, Writing – Review & Editing HS MR ET EV

**Data availability**

Code and data are provided for peer-review at https://figshare.com/s/77f8e0db6053e97b8abd and will be published at the Zenodo repository upon acceptance.

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# Figures

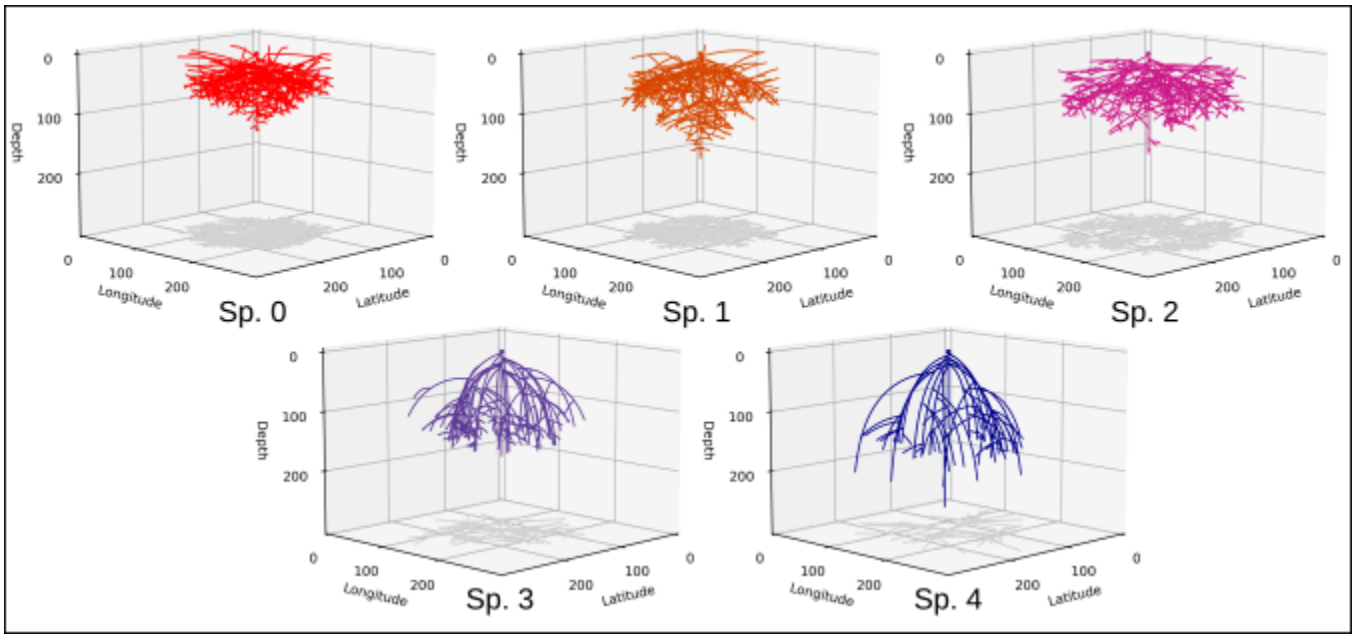



**Figure 1**

Examples of root morphology for the five species. The examples show plants after 150 days of growth in isolation

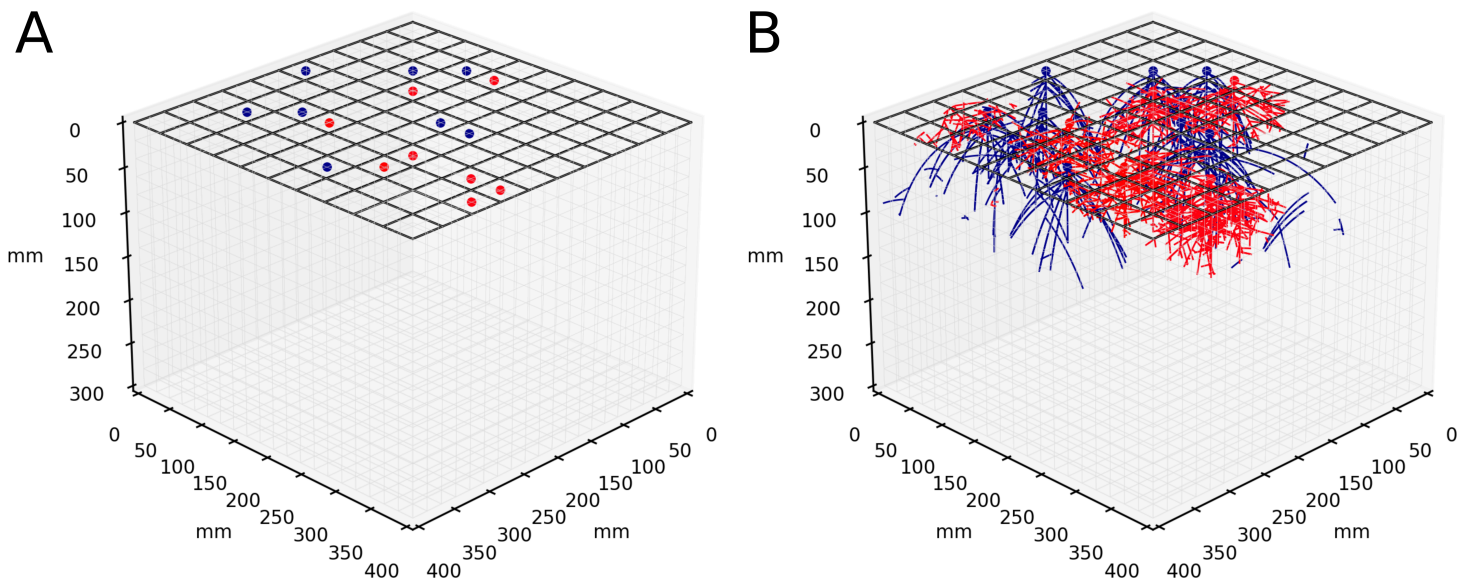



**Figure 2**

Example of a community at the beginning (A) and at time-step 75 (B) of a simulation. The soil is represented as a set of cubic voxels (outline indicated by gray lines). Seeds (dots color coded according to the species) are placed in the centre of cells of a square grid (black lines). At the beginning of simulations, plants have a single root segment and no biomass. As plants gather water from the soil, they grow their roots (coloured lines, red for $Sp_0$ and blue for $Sp_4$) in space according to their genotype. Wrapping in the x and y dimension causes roots to appear disjointed.

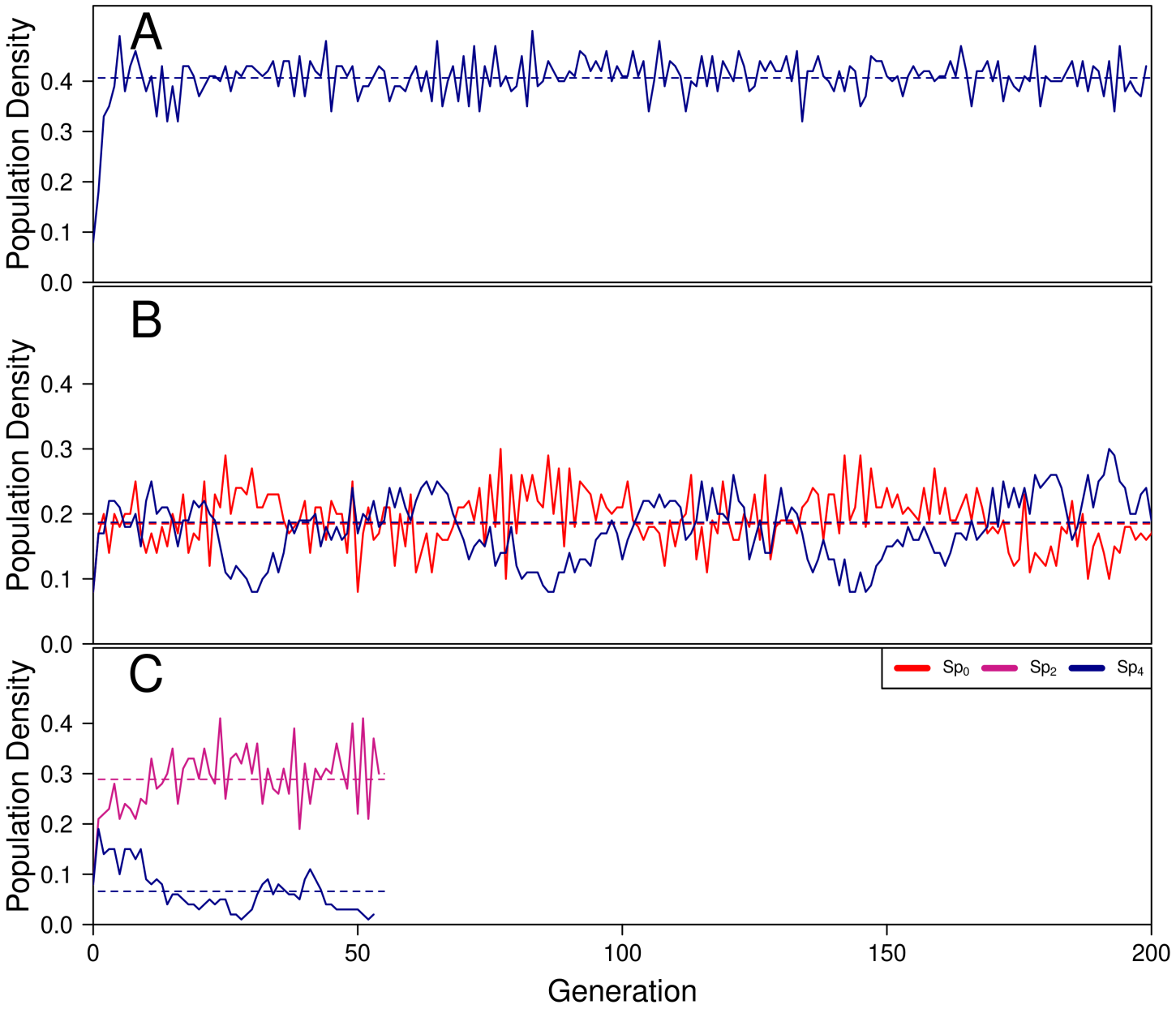



**Figure 3**

Population density per species across generations in three simulation experiments. Population density is the mean number of plants per cell, or (given that each cell can only hold one plant) the proportion of cells occupied by a plant Colours indicate each species; solid lines indicate population density and dashed lines indicate mean population density for the duration of the experiment. The experiments where initialised with the same density per species and included (A) monoculture of Sp4, (B) $Sp_0$:$Sp_4$ , and (C) $Sp_2$:$Sp_4$

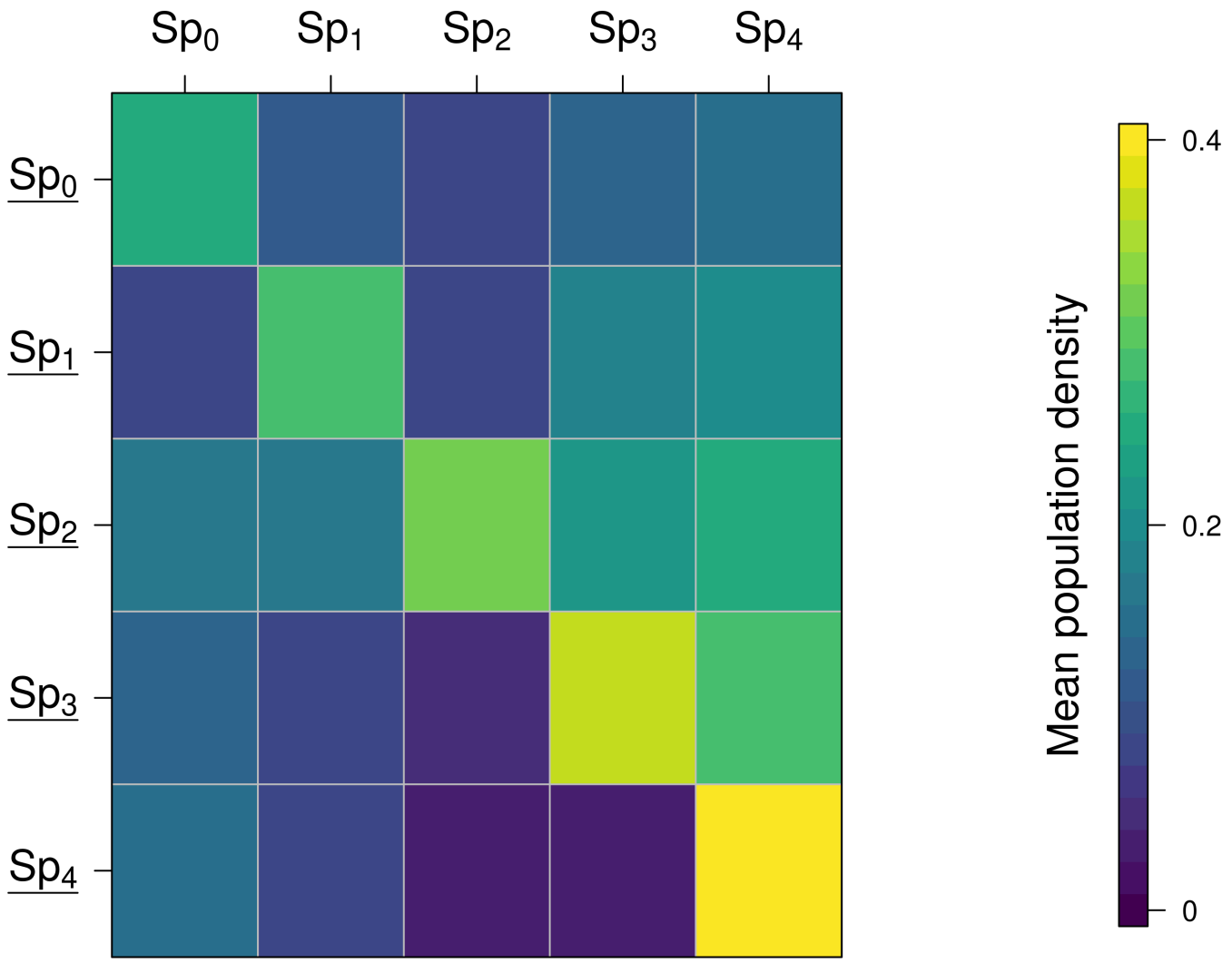



**Figure 4**

Mean population density for the total duration of the experiments. The density corresponds to that of the species name indicated in the grid row name (underlined) in a community including the species indicated by the column name. The diagonal corresponds to the density of a mono-species or neutral community (which are the same as they are functionally identical). The mean was computed for 20 experiment repetitions.

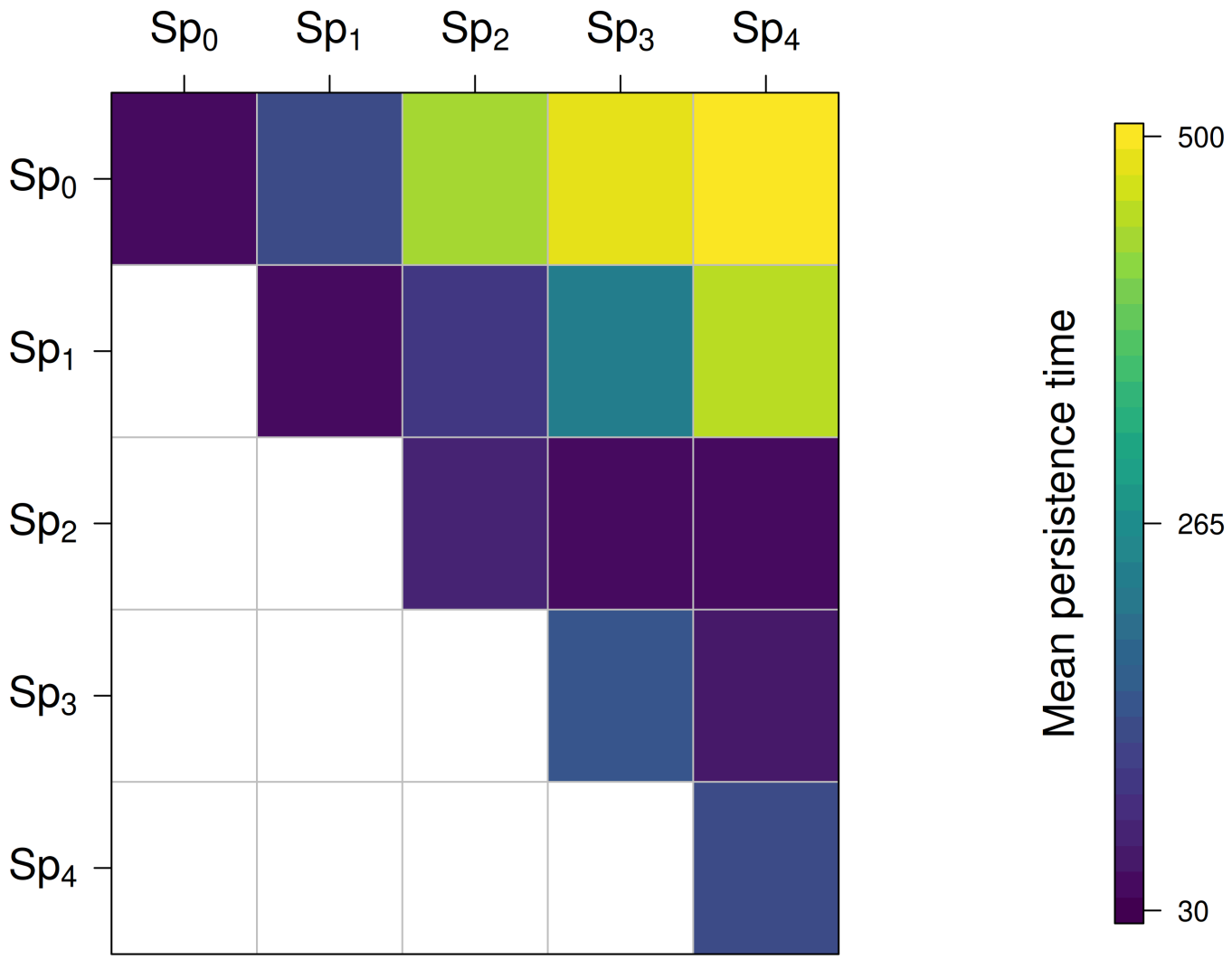



**Figure 5**

Mean persistence time of communities per species pairing over 20 repetitions. The diagonal corresponds to the coexistence of neutral communities

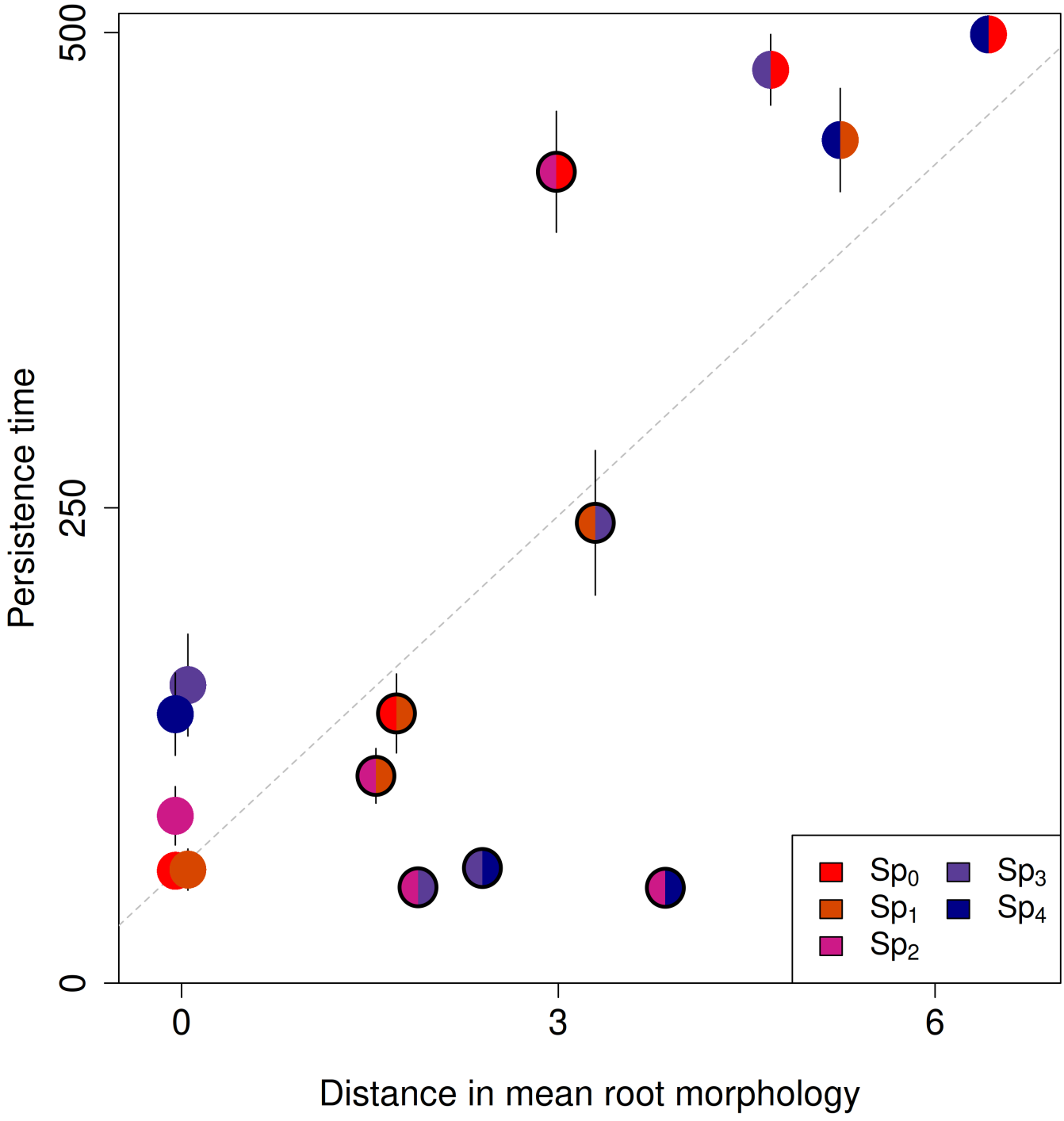



**Figure 6**

Community persistence time as related to contrast in species' root morphology. Contrasts in mean root morphology are shown as the Euclidean distance in the standardised mean root morphology between a pair of species (see text). Persistence time is the number of generations until one species in the community goes extinct. Circles indicate the mean persistence time over 20 replicates and the bar the standard error. The colours of the circles show the two species that comprised the community, single-

coloured circles indicate neutral species communities (see text). Neutral communities all had a distance in mean root morphology of 0, but the position on the x-axis is shown jittered for visibility. The species on the left half (colour) was the one that survived more frequently; circles with a black outline indicate that this species was significantly more likely to persist while the other went extinct. The dashed line indicates the expected persistence time according to a linear model with an estimated slope of 61.58 (p=0.001)

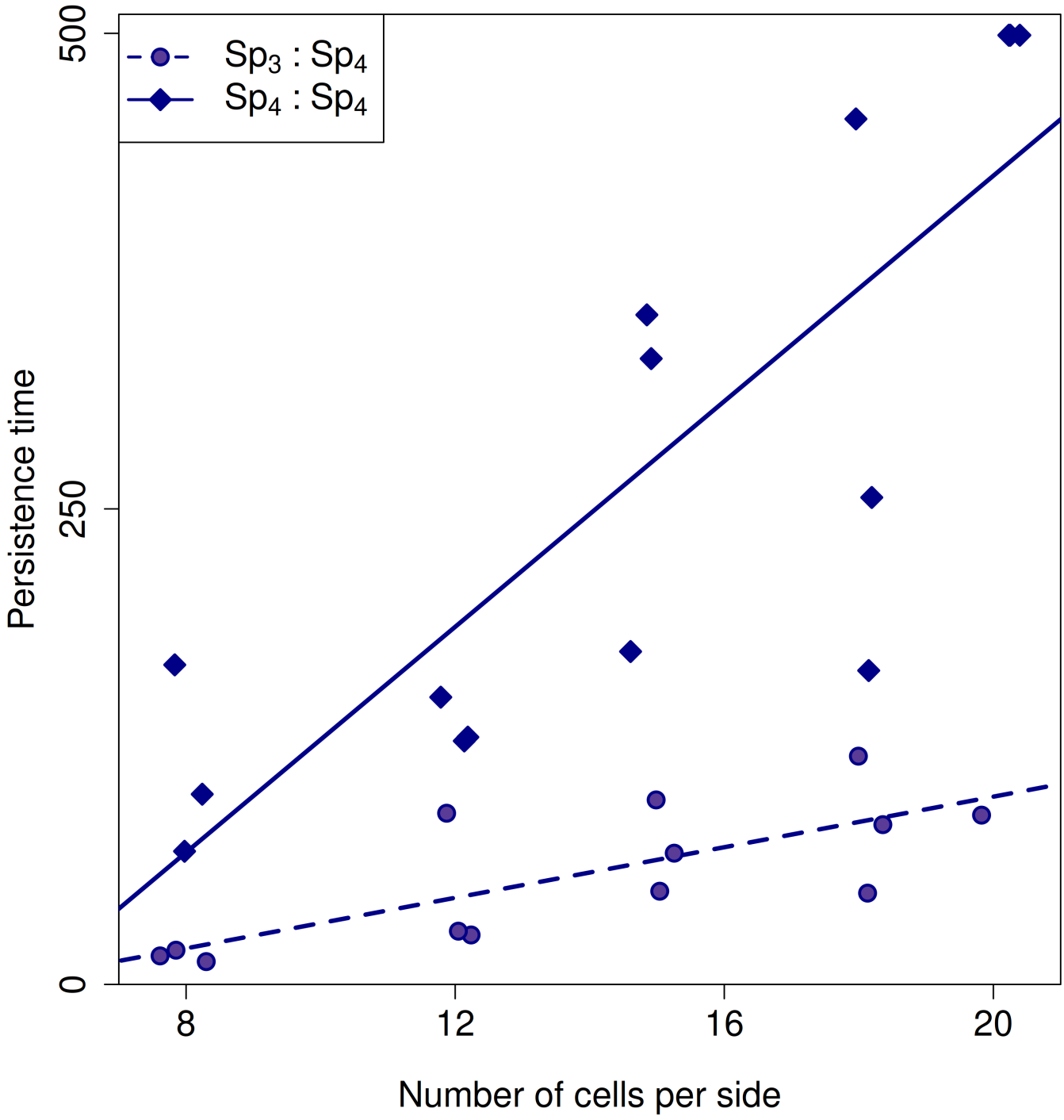


**Figure 7**

Community persistence per grid size for a pair of neutral and non-neutral species. Persistence time is the number of generations until one species in the community becomes extinct. The communities develop in a square grid area composed of 8, 12, 15, 18, or 20 cells per side indicated in x axis. Each point represents an individual simulation; circles correspond to the pair $Sp_3$:$Sp_4$ and diamonds to the pair $Sp_4$:$Sp_4$. The lines indicate the expected persistence time per number of cells per side according to a linear model, with the solid line corresponding to $Sp_3$:$Sp_4$ and the dashed line to $Sp_4$:$Sp_4$.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementarymaterialS1.mp4