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RESEARCH ARTICLE

Toward eco-sustainable afforestation in arid lands: key lessons from a 23-year-old arboretum of native and non-native trees in Jordan

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Abstract

Introduction: Afforestation is a key restoration strategy for mitigating land degradation and desertification in semiarid regions. However, evaluating the ecological impacts of tree species used for sustainable dryland restoration is crucial. For example, non-native tree species may become invasive, with negative effects on native understory biodiversity.

Objectives: This study identifies drought-tolerant tree species suitable for sustainable arid-land afforestation.

Methods: Using 23 years of data from the Jordan University of Science and Technology arboretum, we recorded survival rates and performance (i.e. canopy height and area) of 28 native and 78 non-native tree species under arid conditions. We also assessed their potential for natural spread into surrounding areas; quantified understory species richness and cover.

Results: Native and non-native trees showed comparable survival rates and tree performance, but *Eucalyptus* species outperformed other trees. Four native and 13 non-native species, including seven *Eucalyptus* species, had survival rates above 50% and were designated drought-tolerant. Most native (*Ceratonia siliqua*, *Pistacia atlantica*, and *P. palaestina*) and non-native (*Acacia farnesiana*, *Prosopis chilensis*, and *Tetraclinis articulata*) species had minimal negative impacts on understory diversity. In contrast, *Eucalyptus* species dramatically reduced understory diversity, possibly due to allelopathic effects. *Acacia cyclops* had the highest potential for natural spread.

Conclusions: Our study underscores the importance of balancing drought tolerance with ecological impacts when selecting species for dryland afforestation. Prioritizing native species in restoration efforts can help minimize disruptions to non-forest dryland ecosystems and promote long-term ecological sustainability.

Implications for Practice: Afforestation can be used as a restoration tool in arid regions when suitable species are prioritized and when the site conditions support forest development. Arboreta can serve as vital platforms for guiding such afforestation or urban greening initiatives. In particular, they offer value as long-term, site-specific trials that provide critical insights into the selection of suitable tree species. Science-based strategies that prioritize native or regionally adapted species can enhance ecosystem integrity and improve resilience to climate change. However, careful species selection remains essential to avoid unintended ecological consequences. Non-native species with strong allelopathic effects, such as *Eucalyptus* spp., and species with high spread potential, such as *Acacia cyclops*, should be avoided.

Key words: allelopathy, drought tolerance, *Eucalyptus*, mortality, survival, understory diversity

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Introduction

Arid and semiarid lands cover about one-third of Earth's terrestrial ecosystems (Reisman-Berman et al. 2019; Yıldız et al. 2022) and are among the most fragile due to periodic droughts, erosion, and overexploitation of natural resources (Malagnoux et al. 2007; Rosche et al. 2018). According to the IPBES (2018) assessment, one-third of drylands are degraded, with more than 10 million hectares lost annually (Yıldız et al. 2022). By the end of the twenty-first century, degraded arid lands are projected to expand by approximately 20% (Reisman-Berman et al. 2019), in part due to climate change and increased drought intensity and frequency (Lee; Godfray et al. 2010). Such changes in dryland climate will hasten desertification (Alrababah et al. 2007; Godfray et al. 2010; Al-Gharaibeh et al. 2024).

Restoring degraded drylands is a major challenge for scientists, resource managers, and policymakers (Bainbridge 2017; Wesche et al. 2020; Yıldız et al. 2022). Afforestation has been widely adopted in arid regions to combat desertification, prevent soil erosion, and reduce soil desiccation (Ayyad 2003; Alrababah et al. 2007; Cao et al. 2020). Beyond stabilizing soil, afforestation efforts that prioritize native or regionally adapted species can play a vital role in enhancing ecosystem resilience and promoting sustainability under climate change (Oraon et al. 2023). However, unsuitable afforestation initiatives can alter non-forest habitats, especially in arid and semiarid ecosystems, by reducing light availability and modifying soil properties (Breshears et al. 1998; Ludwig et al. 2004; Alrababah et al. 2007), which can impact understory composition and diversity (Barbier et al. 2008; Wulf & Naaf 2009; Tessema & Belay 2017).

Moreover, several studies have demonstrated that overstory allelopathy can play an important role in shaping understory plant distributions (Mahall & Callaway, 1992; Nilsson & Zackrisson, 1992). Allelopathy refers to chemically mediated interference competition between neighboring plant species, encompassing both direct effects of the chemicals and indirect effects of the chemicals mediated through interaction with soil microbial or fungal communities (Inderjit & del Moral, 1997).

Dryland afforestation often prioritizes drought-tolerant, fast-growing species with high establishment success, while neglecting potential ecological risks, especially from non-native species (Dov et al. 2001; Reisman-Berman et al. 2019). Non-native species often exert stronger effects on biodiversity than native species and potentially outcompete native flora and threaten local biodiversity (Richardson & Pyšek 2006; Shah et al. 2014; Davis et al. 2019). Additionally, non-local species, including native and non-native species, may spread beyond plantations and compete with native flora and threaten ecosystem stability (Reisman-Berman et al. 2019; Ravhuhali et al. 2021). For example, non-native *Eucalyptus* species are widely planted in arid regions due to their drought tolerance (Reisman-Berman et al. 2019). Their rapid growth and high biomass production contribute to their plantation success across diverse environments and soil types (Saadaoui et al. 2017). In the *Eucalyptus* genus, leaves contain allelochemicals such as phenolic derivatives and terpenoids (Zhang & Fu 2009; Silva et al. 2017). These substances can be released from leaf litter through volatilization or leaching by rainfall (Kaur et al. 2011) and have been shown to directly inhibit seed germination and early seedling development (Chu et al. 2014; Zhang et al. 2024). Similarly, *Pinus halepensis*, native to the Middle East and used in dryland afforestation, can reduce biodiversity in non-native ranges (Bellot et al. 2004; Alrababah et al. 2007).

The resilience of dryland ecosystems is closely linked to maintaining biodiversity (West 1993; Tilman & Downing 1994). Therefore, understanding how afforestation impacts biodiversity in arid regions is critical for sustainable restoration (Alrababah et al. 2007; Tessema & Belay 2017; Reisman-Berman et al. 2019), as these impacts vary widely depending on the overstory species (Barbier et al. 2008; Wulf & Naaf 2009; Jagodzinski et al. 2015). Long-term assessments are essential, as ecosystem changes often emerge decades after afforestation (Dickie et al. 2006; Hobbie et al. 2007; Barbier et al. 2008); yet such data remain scarce, especially for the arid Irano-Turanian bioclimatic region. Arboreta, with their controlled settings and diverse species collections, can offer valuable insights into native and non-native tree species' drought tolerance and their impacts before they are used in large-scale afforestation (Carrillo-Gavilan & Vila 2010; Fanal et al. 2021).

In Jordan, forests cover less than 1% of the national territory (Qarallah et al. 2021) and are confined mainly to the Mediterranean bioclimatic region (see Zohary 1973 for conceptual details on bioclimatic regions in the Middle East). According to Al-Eisawi (1996), the Mediterranean bioclimatic region receives the highest annual rainfall (400–600 mm) and has the most fertile soils. It also experiences the mildest summer temperatures, rarely exceeding 30°C, and supports the country's richest vegetation cover. In contrast, over 90% of Jordan falls within the arid Irano-Turanian and Saharo-Arabian bioclimatic regions, which are marked by lower rainfall, higher temperatures, and more widespread land degradation (Zohary 1973; Al-Eisawi 1996; Al-Gharaibeh et al. 2017). Since the 1950s, Jordan's Department of Forestry has implemented afforestation projects, establishing approximately 46,000 ha of new forests (Ministry of Agriculture 2022). Most of their initiatives are confined to the boundary of the Mediterranean bioclimatic zone, rely heavily on a limited number of native and non-native species, with *P. halepensis* (native) and *Eucalyptus camaldulensis* (non-native) among the most frequently planted. Recent initiatives have expanded into drier regions, focusing on the Irano-Turanian transitional zone, a key front in combating desertification. Despite these efforts, species trials in this arid region remain limited.

We used the Jordan University of Science and Technology (J.U.S.T) Arboretum and its extensive collection of native and non-native species to assess tree species' suitability for dryland afforestation. Specifically, the objectives of this study were to: (1) identify drought-tolerant species and (2) assess their performance (survival, canopy cover and height) after 23 years; (3) detect the potential for natural spread by evaluating the spontaneous establishment of all planted species under the local conditions; and (4) examine the canopy impact of designated

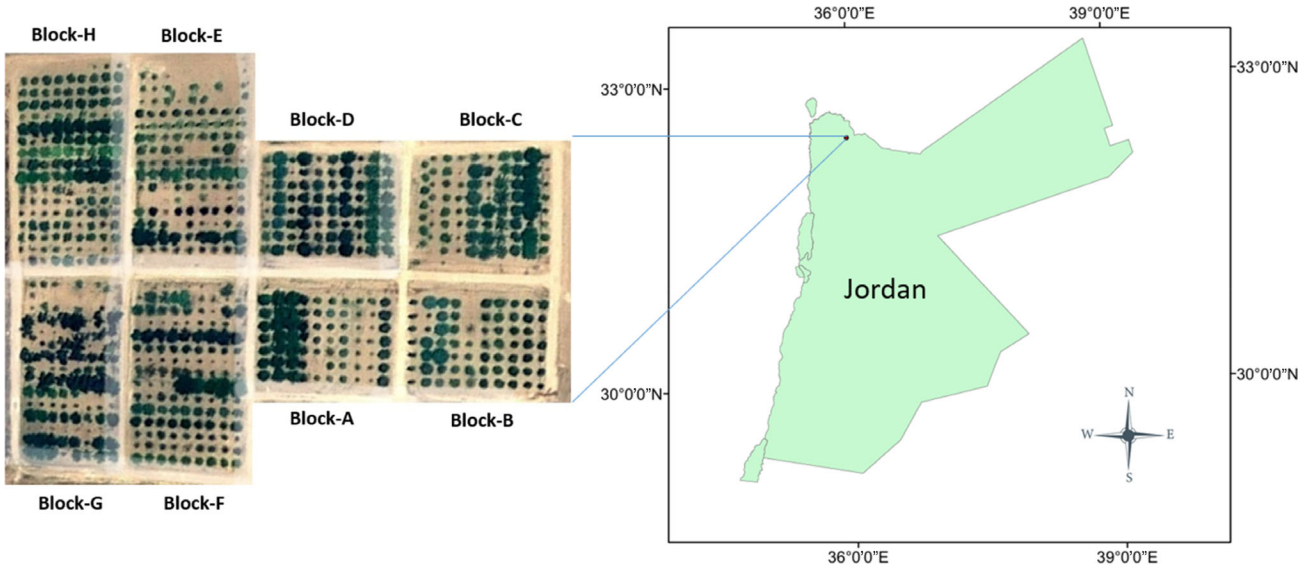


Figure 1. Location and design of the Jordan University of Science and Technology arboretum.

drought-tolerant species on understory diversity, composition, and ecosystem integrity. We specifically compared native and non-native species, with a focus on *Eucalyptus* species, to inform eco-sustainable afforestation, enhance ecosystem resilience, and support habitat restoration in arid lands.

Methods

Site Description

The J.U.S.T. arboretum was established in 2001 in Irbid, Jordan (32°34′N; 36°01′E), approximately 500 m above sea level. The campus is situated in the northeastern semiarid grasslands of Jordan (Fig. 1) and lies at the convergence of two bioclimatic regions: Mediterranean and Irano-Turanian. This intersection creates a semiarid ecotone that enhances the diversity of flowering plant species (Al-Gharaibeh 2005). Since its establishment in 1976, the vegetation cover on the J.U.S.T. campus has been protected from grazing livestock (Al-Gharaibeh 2005).

The arboretum is characterized by flat to gently rolling topography with slopes of less than 8% (Alrababah et al. 2007). The site has an arid climate with mild, rainy winters and dry, hot summers. The mean annual precipitation is 210 mm, while the mean maximum temperature during the hottest dry months (June–September) was 40°C over the past 24 years (Table S1). The soil is fine-loamy, mixed, thermic, and alkaline, with a pH of 8.03, electrical conductivity (EC) of 0.78, and nitrogen content (N%) of 0.25.

By hosting over 100 different tree species from 29 families, this arboretum is the largest educational living collection of native and introduced tree species in the Levant. The planting site covers 220 m in length (east–west direction) and 190 m in width, totaling 42,000 m^2. The arboretum is systematically designed, with the entire area divided into eight blocks (A–H) by a network of 3-m-wide roads (Fig. 1). Each block is divided into rows, with most rows containing a single species.

Irrigation Regimes and Drought Phases

The arboretum was equipped with a drip irrigation system designed to meet the water requirements of the trees, particularly during the dry months from May to October. Over time, the irrigation regime underwent significant changes that influenced the survival, adaptability, and resilience of the planted tree species under escalating drought stress conditions, resulting in three distinct phases:

(1) *The establishment phase (2001–2009)*: During this phase, a standard irrigation regime was implemented to ensure successful tree establishment. Trees were irrigated twice per week, with each tree receiving approximately 20 L per irrigation event, regardless of species or age.
(2) *The moderate drought phase (2010–2019)*: This phase marked a transitional period characterized by moderate watering due to a water supply shortage at J.U.S.T. Trees were irrigated once per week, with each tree receiving approximately 20 L per week, regardless of species or age.
(3) *The intensified drought phase (2020–2024)*: In this phase, irrigation ceased entirely due to significant damage to the irrigation infrastructure, compounded by the coronavirus disease of 2019 (COVID-19) lockdown in 2020. As a result, trees were fully exposed to natural drought conditions. This phase provided the opportunity for insights into the long-term drought tolerance and survival potential of the various species.

Sampling and Data Collection

Survival and Identification of Drought-Tolerant Tree Species. Tree survival was assessed at the end of the 2009, 2019, and 2024 growing seasons. For each species, the number of surviving individuals was recorded, and the final survival (FS) percentage by 2024 was calculated as:

$$FS\% = \frac{n_{s\text{-}2024}}{n_p} \times 100\%$$

where: $n_{s\text{-}2024}$: The number of surviving individuals in 2024 and n_p: The total number of planted individuals in 2001.

Tree species whose aboveground parts died completely each season but exhibited coppicing were classified as dead.

The FS percentage, which is 100% minus the mortality percentage, was used to identify drought-tolerant species. Based on the classification by Kulha et al. (2023), which categorizes drought tolerance levels according to mortality rates, ranging from 44% (low tolerance) to 16% (high tolerance), species with an FS percentage exceeding 50% were considered promising drought-tolerant candidates in this study.

Performance of the Drought-Tolerant Tree Species. We assessed canopy growth performance for all species identified as drought-tolerant during the 2024 growing season, including average height and average projected crown cover. Tree height was measured using the Crain Measuring Ruler, while canopy diameter was measured in north–south and east–west directions using a measuring tape at ground level. An ellipse approximation of the canopy was utilized to calculate the vertical projected crown cover for each tree, following the formula outlined by Tessema and Belay (2017).

Spontaneous Spread of Arboretum Species. A critical indicator of the invasiveness of non-native tree species is their capacity to spread spontaneously (Reisman-Berman et al. 2019). To assess spread, a comprehensive survey was conducted in 2024 across areas surrounding the arboretum. The absence of agricultural activities within 1000 m of the arboretum created an ideal setting for evaluating spontaneous spread. During the survey, the number of individuals per species, their height, and their distance from the arboretum boundaries were recorded. The survey area was divided into systematic distance intervals of 200 m: 0–200, 200–400, 400–600, 600–800, and 800–1000 m from the arboretum borders. Recorded individuals were classified as: saplings (up to 0.5 m in height), shrubby trees (0.5–5 m in height), or trees (above 5 m in height). For each distance interval, the number of individuals per species within each height category was documented. Importantly, none of the recorded species had been planted or naturally occurred in the survey area prior to the establishment of the arboretum.

Impact on Understory Biodiversity. To assess the impact of identified drought-tolerant tree canopies on understory biodiversity, species diversity indices (Shannon diversity and species richness) and understory vegetation coverage were assessed both beneath (inside) and outside the canopy. Sampling was conducted exclusively under drought-tolerant tree species with a canopy spread exceeding 2 m in all directions and a minimum of five surviving individuals. A systematic sampling approach using 1-m^2 quadrats was employed for both canopy conditions (Fig. 2). Within each quadrat, all plant species were identified, including arboretum tree seedlings shorter than 15 cm. The number of individuals per species and their total coverage were recorded. For sampling beneath the canopy, a transect was established along each row of tree species, intersecting the trunks. Two quadrats were placed between each surviving tree pair: one positioned 1.5 m away from the trunk of the first tree, and the second 1.5 m before the trunk of the next tree. Due to overlapping canopies along most tree lines, a parallel transect was established on each side of the arboretum borders to assess the vegetation composition beyond the canopy. Quadrats were evenly spaced along these transects. The number of quadrats within the canopies varied depending on the number of surviving trees per line, ranging from 10 to 16. Outside the canopies, the number of quadrats was standardized to the highest number used within any tree line, which was 16.

Statistical Analysis

All statistical analyses were conducted in R version 4.3.3 (R Core Team 2024). For our univariate data, we ran (generalized) linear mixed-effects models (GLMMs) using the R package lme4 1.1-35.1 (Bates et al. 2015). Model significance was evaluated using likelihood ratio tests. Multivariate analyses were conducted with the R package vegan 2.6-8 (Oksanen et al. 2024).

To analyze the survival data, we used a GLMM with survival modeled as a binary outcome with a binomial error distribution. The fixed effects included origin (native vs. non-native vs. *Eucalyptus* species) and year of survey, as well as their interaction. Given the distinct survival patterns, growth performance, and understory impact of *Eucalyptus* species, non-native species were further divided into non-*Eucalyptus* and *Eucalyptus* groups. Random effects accounted for variation among blocks (A–H), position within the blocks (edge vs. not edge), and the nested structure of species nested within family nested within leaf type (broadleaves vs. conifers). This approach allowed us to assess the influence of tree origin and time on survival while accounting for spatial dependencies in the data, potentially confounding edge effects, and hierarchical pseudo-replication within phylogenetic groups. Pairwise comparisons between the three origin types of the tree species were conducted within each survey year. Ten species that experienced complete mortality during the establishment phase (100% by 2009; Table S2) were excluded from survival analyses for 2019 and 2024.

For tree species classified as drought-tolerant, we evaluated whether their growth performance differed between native and non-native trees and specifically *Eucalyptus* species using two linear mixed-effects models (LMMs) with the following response variables: $\log_e$-transformed canopy area and $\log_e$-transformed tree height. The structure of the random effects in these models was identical to that used in the GLMM analyzing the survival data. To investigate differences among individual tree species, we ran the same models with species as a fixed factor instead of plot type. Tukey–Kramer honestly significant difference (HSD) was applied for species mean separation.

Three additional LMMs were calculated to analyze our univariate herbaceous vegetation data, using the same structure as the performance models. However, instead of the factor "origin," we used "plot type" (native vs. non-native trees vs. *Eucalyptus*

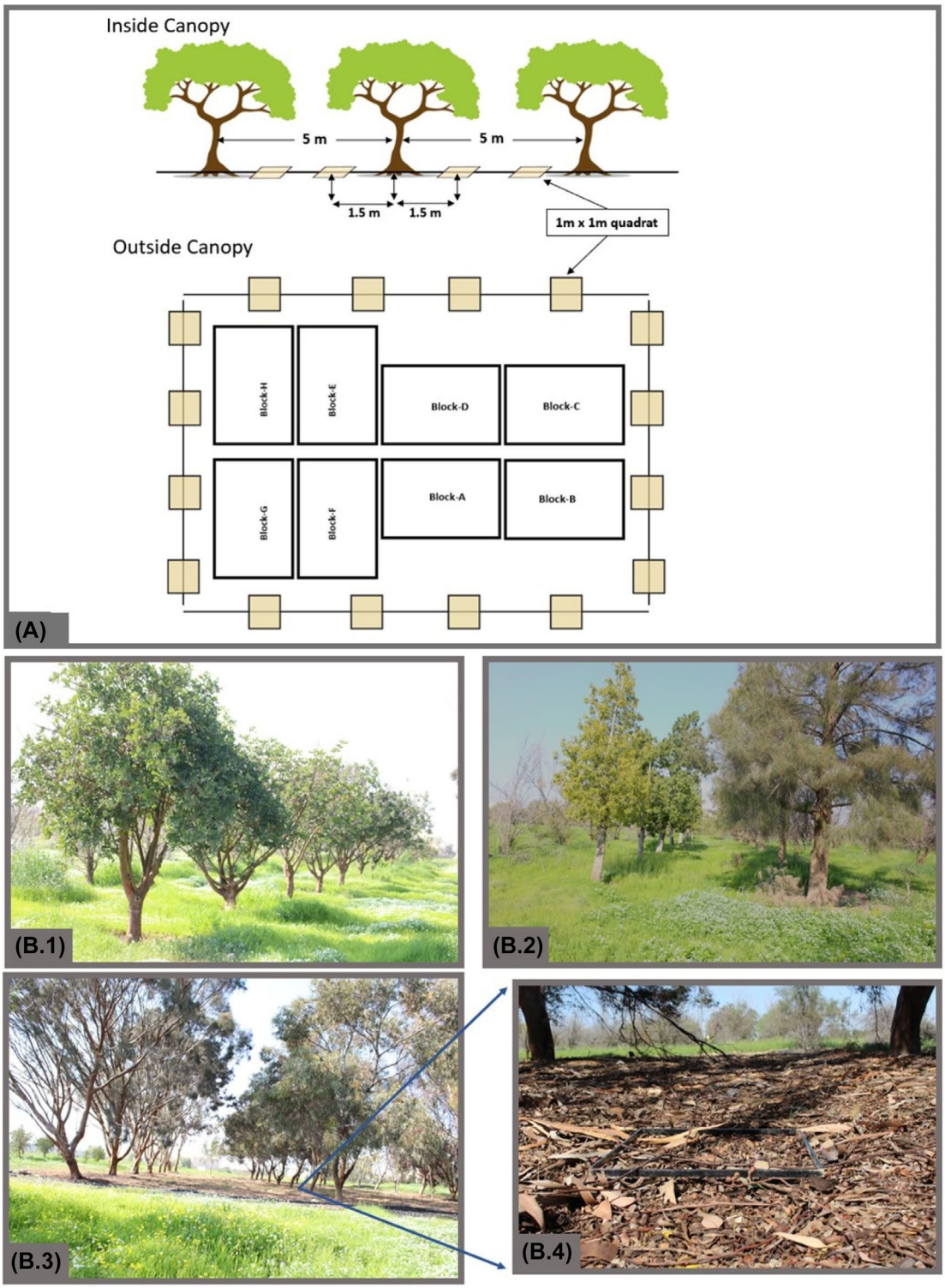


Figure 2. Native and non-native tree canopies and their understory vegetation. (A) Sampling design for data collection inside and outside tree canopies at the Jordan University of Science and Technology Forestry Arboretum, northern Jordan. (B.1–4) Photographs illustrating the varying apparent impacts of different tree species on understory vegetation: (B.1) minimal apparent impact under the native species *Ceratonia siliqua*, (B.2) moderate impact under the non-native species *Casuarina equisetifolia* and *Brachychiton populneus*, (B.3) strong apparent negative impact under non-native *Eucalyptus* species, and (B.4) close-up of ground cover beneath the *Eucalyptus* canopy, showing the quadrat used for recording herbaceous species and their percent cover.

species vs. control plots located outside the arboretum). The random effect of edge was not included because we did not record vegetation surveys at the outer range of the tree at the edges of the blocks (see Fig. 2). The following three response variables were analyzed: logit-transformed total cover within plots, species richness, and Shannon diversity. We investigated differences among individual tree species with the same model and Tukey–Kramer HSD as for the analysis of tree performance.

To examine whether the composition of plant communities differed between plot types (native, non-native, and control plots located outside the arboretum), we performed a non-metric multidimensional scaling (NMDS) analysis based on Bray–Curtis distances. NMDS was chosen over other multivariate methods, such as principal coordinates analysis, due to the very high proportion of zero entries in the vegetation data (Minchin 1987). However, because zero frequency was particularly high (89.7%), the NMDS had a relatively high stress value (0.257). Thus, we also calculated the NMDS using three dimensions, which yielded a moderate stress value (0.175). A Permutational Multivariate Analysis of Variance (PERMANOVA) was calculated with 10,000 permutations using pairwise Bray–Curtis distances among plots and plot type as the response variable. All *Eucalyptus* species were excluded from our multivariate analyses (NMDS, PERMANOVA) because of the very low cover of the herbaceous layer ($\text{mean}_{\text{Species richness}} = 0.76 \pm 0.85$; $\text{mean}_{\text{Total Cover}} = 0.78 \pm 0.89$).

Results

Survival and Identification of Drought-Tolerant Tree Species

Of the 788 planted trees, 76.8% survived in 2009, 39.2% survived in 2019, and 20.2% survived in 2024. Native and non-native trees exhibited a mean survival rate of 46.2% and 45.1%, respectively. Within the non-native trees, *Eucalyptus* species had a 90.8% survival rate vs. other non-native trees at 41.6%. We consequently analyzed these as two different groups. The three groups (native, *Eucalyptus*, other non-native) differed significantly in how their survival rates changed over time ($\chi^2 = 7.58$, $p < 0.001$, Fig. 3).

In 2009, that is, 9 years after planting, 13 out of 28 natives, 30 out of 70 non-natives, and 5 out of 8 *Eucalyptus* species showed a survival of 100%. Overall, however, the mean survival of native (80.9%), non-native (73.8%), and *Eucalyptus* (92.5%) trees did not differ significantly from one another in the establishment phase. The impact of reduced irrigation during the moderate drought phase (2009–2019) led to a substantial decrease in total survival, with 55 of the 106 tree species exhibiting mortality rates of 50% or more, and 31 of those species already reaching 100% mortality. After the moderate drought phase, mean survival of native trees (36.9%) was comparable to that of non-native trees (36.1%) but both groups showed significantly lower survival than *Eucalyptus* species (92.5%). During the subsequent 5 years of the intensified drought phase (2019–2024), an additional 21 species reached 100% mortality (Table S2), including, for example, the commonly drought-tolerant native *Pinus halepensis*. The number of species with mortality rates of 50% or higher was 87 (24 native, 54 non-native, and one *Eucalyptus* species). These results reflect the significant impact of prolonged water scarcity on the survival of both introduced and native tree species in the arboretum. Overall, mean survival of native (20.9%) and non-native (14.7%) trees did not differ significantly after 23 years growth in the arboretum. However, both groups showed significantly lower survival than the *Eucalyptus* trees (mean = 87.5%).

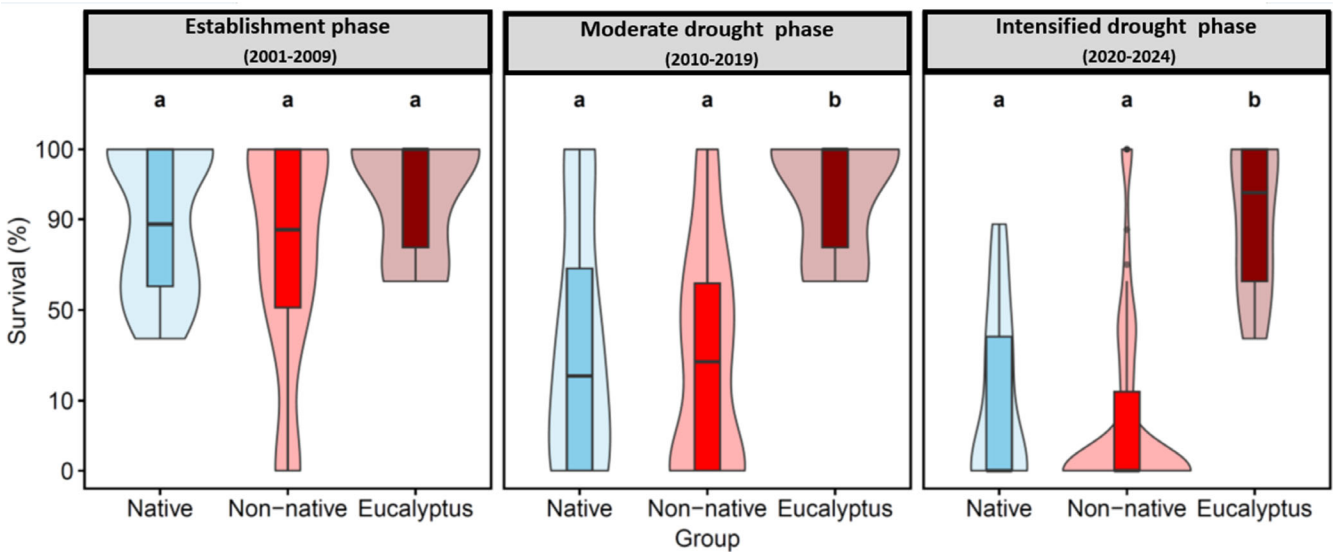


Figure 3. Survival percentage of native (blue), non-native (red), and *Eucalyptus* (dark red) trees in the arboretum at the end of the three phases (establishment, moderate drought, and intensified drought). Note that the *y*-axis (survival) is logit-scaled as the data were analyzed using a generalized linear model with binomial error distribution. Letters above the violin plots indicate post hoc results from pairwise comparisons with a significance threshold of p less than 0.05.

Table 1. List of designated drought-tolerant tree species with survival percentages exceeding 50%, including the average canopy area and average height of surviving individuals. Leaf type B: broadleaves; C: conifers; $n_{p\text{-}2001}$: number of individuals planted per species in 2001; $n_{S\text{-}2024}$: number of surviving individuals per tree species in 2024. AH, average height of surviving individuals; APCA, average projected crown cover of surviving individuals; FS%, final survival percentage at the end of the 2024 growing season.

Species	*Leaf type*	$n_{p\text{-}2001}$	$n_{s\text{-}2024}$	*FS%*	*APCC (m^2)*	*AH (m)*
Native						
Ceratonia siliqua	B	9	7	77.8	15.74	4.33
Juniperus phoenicea	C	7	6	85.7	23.22	6.7
Pistacia atlantica	B	9	8	88.9	11.25	4.17
P. palaestina	B	9	7	77.8	9.94	3.67
Non-native						
Acacia cyclops	B	9	9	100	37.75	6.77
A. farnesiana	B	9	9	100	11.26	3.67
Brachychiton populneus	B	8	7	87.5	12.21	5.67
Casuarina equisetifolia	B	8	6	75	36.68	10.5
Prosopis chilensis	B	6	6	100	72.86	5.67
Tetraclinis articulata	C	7	7	100	15.04	7
Eucalyptus species						
Eucalyptus camaldulensis	B	6	6	100	44.63	11.1
E. occidentalis	B	3	2	66.7	42.34	12.6
E. spathulata	B	6	6	100	74.11	11
E. stricklandii	B	6	6	100	136.01	14.17
E. torquata	B	6	6	100	59.39	6.33
E. wandoo	B	7	6	86	42.71	10.97
E. woodwardii	B	3	2	66.7	39.7	13.2

Among the 28 native species that were initially planted, the highest survival rate was recorded for *Pistacia atlantica* (88.9%). Among the 78 non-native species, eight had 100%, including *Acacia cyclops*, *A. farnesiana*, *Prosopis chilensis*, and *Tetraclinis articulate*, and four out of eight planted *Eucalyptus* species—*E. camaldulensis*, *E. spathulata*, *E. stricklandii*, and *E. torquata*. Tree species with survival rates exceeding 50% were classified as drought-tolerant, resulting in a subset of 18 species (four native, seven *Eucalyptus*, and six other non-native trees, Table 1). This group included the aforementioned species, along with the native *Ceratonia siliqua*, *Juniperus phoenicea*, and *P. palaestina*, as well as the non-native *Brachychiton populneus*, *Casuarina equisetifolia*, *E. occidentalis*, *E. wandoo*, and *E. woodwardii*.

Performance of the Drought-Tolerant Tree Species

Within the designated drought-tolerant tree species, the *Eucalyptus* trees had a significantly greater canopy area ($\chi^2 = 7.85$, $p = 0.02$; Table 1; Fig. 4A) and tree height ($\chi^2 = 6.18$, $p = 0.045$, Fig. 4B) than the native species and other non-native species. Breaking it down to species (Fig. S1), *E. stricklandii* showed the largest canopy area (mean = 136.01 m^2) and the tallest height (mean = 14.17 m), while the native tree *P. palaestina*

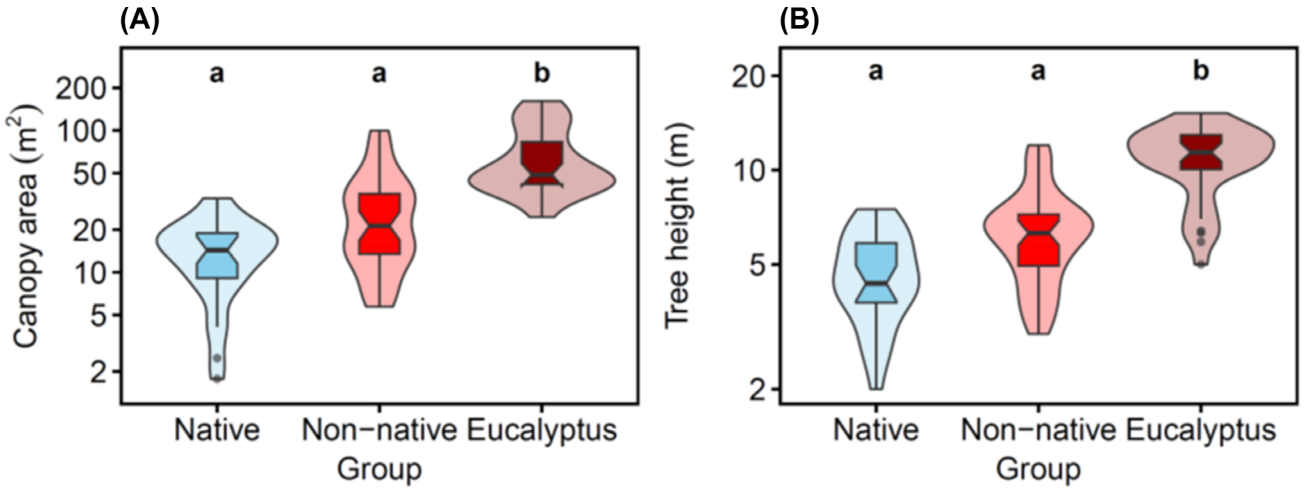


Figure 4. Performance of native (blue), non-native (red) and *Eucalyptus* (dark red) trees in the arboretum. (A) Canopy area (in square meters) and (B) tree height (in meters) both differed significantly between the three groups of tree species. Canopy area and tree height data are log-scaled as they have been loge-transformed in the statistical analyses. Letters above the violin plots indicate post hoc results from pairwise comparisons with a significance threshold of p less than 0.05.

exhibited the smallest canopy cover (mean = 9.94 m^2) and shortest height (mean = 3.67 m).

Spontaneous Spread of Arboretum Species

Five out of the 106 planted tree species escaped the arboretum, spread, and established at varying distances in the surrounding area (Fig. 5). These species were all non-native, including *Acacia cyclops*, *A. saligna*, *A. victoriae*, *Ailanthus altissima*, and *B. populneus*. Since these species were planted exclusively within the arboretum and are not found in other locations within or beyond the J.U.S.T. campus (4.5 km × 7.5 km), their spread can likely be attributed to propagules originating from the arboretum. The number of individuals of all species combined declined with increasing distance from the arboretum. *Acacia cyclops* exhibited the greatest spread distance, with seven individuals observed up to 5 km beyond the arboretum boundaries, primarily in untilled spots with available water sources, such as irrigation or water leakage points. *Acacia cyclops* spread the most in terms of numbers across different distance intervals, particularly for sapling and shrubby tree categories. *Ailanthus altissima* showed the highest number of individuals for the tree category at distances ranging from 600 to 1000 m. The other three species, *B. populneus*, *A. saligna*, and *A. victoriae*, were present in the surrounding area but at very low numbers and limited distances beyond the arboretum borders.

Impact on Understory Biodiversity

A total of 62 plant species from 16 families were recorded in the herb layer both inside and outside canopy areas. Among the 62 recorded species, 23 were found both under and outside canopy areas, while 18 species were exclusive to under canopies and 21 to outside canopies (Table S3). Notably, the following ruderal species were found exclusively beneath non-native tree canopies: *Sonchus oleraceus*, *Solanum nigrum*, and *Urospermum picroides*. Overall, the vegetation composition differed significantly between the control plots outside the arboretum, beneath the native tree species, and beneath the non-native tree species (pseudo-$F = 7.06$, $p < 0.001$, Figs. 6A & S2). Pairwise comparisons revealed significant differences in vegetation composition among all three groups. *Eucalyptus* species were excluded from the multivariate analyses because there was minimal vegetation cover below them (Fig. S3).

Species richness differed significantly between the plot types ($\chi^2 = 24.02$, $p < 0.001$, Fig. 6B). All three tree species groups had lower numbers of herbaceous species compared to the control. *Eucalyptus* species had a significantly lower species richness than the native trees and the other non-native tree species. Species richness under most tree species considered separately was comparable to that of the control plots, with the exception of *Eucalyptus* species, *J. phoenicea*, and *A. cyclops* (Fig. S4a). All *Eucalyptus* species had lower species richness in their understories compared to all other tree species and the control plots.

A similar pattern was found for the Shannon diversity index, which also significantly differed between the plot types ($\chi^2 = 20.99$, $p = <0.001$, Fig. 6C). However, at the individual tree species level, except for *Eucalyptus* species and *B. populneus*, no significant differences in diversity were observed between the tree plots and the control plots (Fig. S4b). More specifically, *Eucalyptus* species consistently

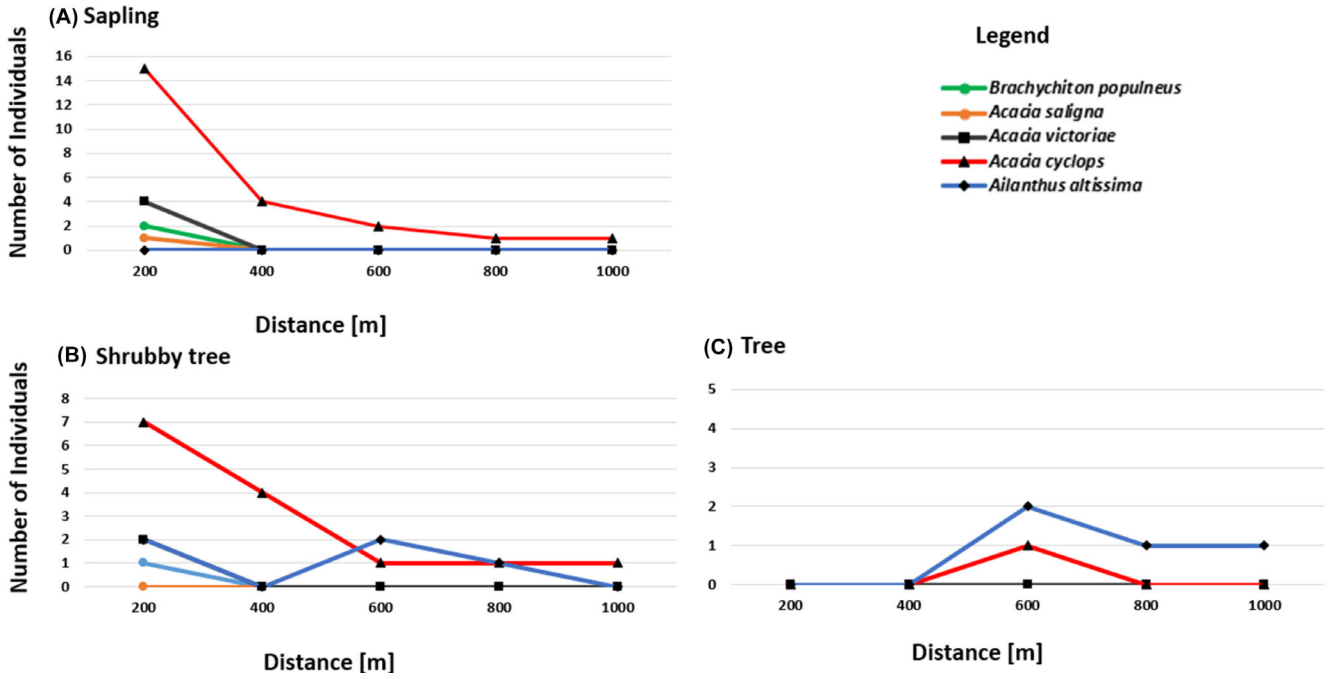


Figure 5. Number of individuals per species at 0–200, 200–400, 400–600, 600–800, and 800–1000 m from the arboretum borders, classified into three categories based on individual height: (A) sapling: up to 0.5 m, (B) shrubby tree: 0.5–5 m, and (C) tree: over 5 m.

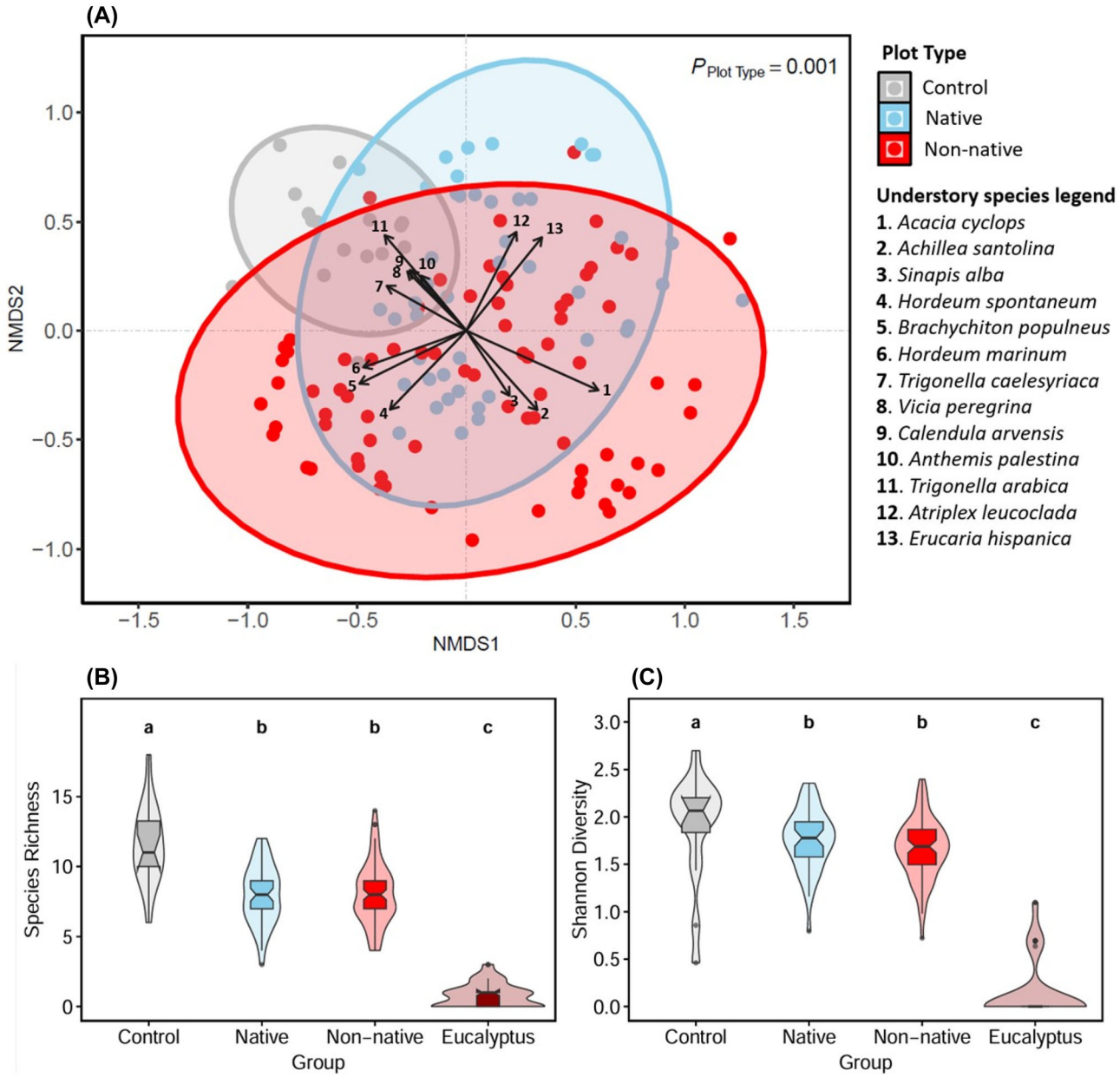


Figure 6. Effect of native (blue), non-native (red), and *Eucalyptus* (dark red) trees on the community composition and species diversity of the herbaceous layer. Control plots (gray) were located outside the arboretum. (A) The NMDS was calculated based on 62 understory species. Of these, 13 species showed a highly significant correlation with the multivariate pattern (using the envfit function, indicated as vectors; see legend). The presented p-value was based on a PERMANOVA. Note that all Eucalyptus species were excluded from our NMDS because there was minimal vegetation cover in the herbaceous layer below them (Table S3). (B and C) Univariate comparisons among the four groups for (B) species richness, and (C) Shannon diversity of the understory vegetation. Letters above the violin plots indicate post hoc results from pairwise comparisons among the three different groups with a significance threshold of p less than 0.05.

exhibited lower herbaceous diversity in their understory compared to all other tree species.

Discussion

In arid environments, extreme droughts are arguably the primary drivers of tree growth (Williams et al. 2012; Hammond et al. 2022; Glatthorn et al. 2024). At the J.U.S.T. Arboretum, we planted 106 tree species to investigate their potential for afforestation. Most of them were planted outside their natural distribution, and despite irrigation during establishment, local climate and soil conditions imposed an early and distinct filtering effect on the survival and performance of the study species (Villegas et al. 2020, Berhe et al. 2024). While non-native species may succeed due to various ecological and physiological advantages (Reisman-Berman et al. 2019), this study

specifically examined how species origin influences their suitability for afforestation.

Survival and Identification of Drought-Tolerant Tree Species

Drought-induced mortality is widely recognized as a major factor shaping forest structure (Herrero et al. 2023), especially in arid regions (Grossiord et al. 2014). During the moderate drought phase, irrigation reduction caused higher tree mortality rates compared to the establishment phase. The complete cessation of irrigation during the intensified drought phase further exacerbated drought stress, particularly during the hot, dry summer months, a critical period for tree survival. Competition for water can intensify mortality (Ruiz-Benito et al. 2013; Young et al. 2017; Rebollo et al. 2024) and may have been a factor in our relatively dense 5-m planting layout, as previous research has found similar spacing amplifies water scarcity in arid regions (Hébert et al. 2016; Bradford et al. 2022). Even native drought-tolerant species were affected under these conditions. *Pinus halepensis*, a widely recommended afforestation species in arid Mediterranean regions (Bellot et al. 2004; Alrababah et al. 2007; Reisman-Berman et al. 2019), exhibited strong growth until the intensified drought phase, when it suffered 100% mortality. This result underscores the impact of prolonged water stress, even on presumed tolerant species.

Long-term monitoring is essential for accurately assessing survival, and thus drought tolerance in afforestation projects (Reisman-Berman et al. 2019). Non-native species, particularly *Eucalyptus*, exhibited the highest survival rates (100%), likely due to their diverse morphological, physiological, and nutritional adaptations that enable a combination of drought avoidance, escape, and tolerance (Saadaoui et al. 2017). Three other drought-tolerant species belonged to the genera Acacia and Prosopis, both of which originate from arid regions and are widely cultivated in arid environments (Ravhuhali et al. 2021; Uni et al. 2023). *Tetraclinis articulate* was previously known for its tolerance to semiarid Mediterranean conditions (Rozas et al. 2021), but our survey is the first documented drought resilience success in such arid conditions.

Among native tree species, *Pistacia atlantica* exhibited the highest survival. The chorotype of this species is the Irano-Turanian bioclimatic region, which experiences higher temperatures and lower rainfall compared to the Mediterranean biogeographical region (Al-Eisawi 1996; Al-Gharaibeh 2005; Al-Gharaibeh et al. 2017). In contrast, although *P. palaestina* is from the same genus, its distribution is limited to the Mediterranean bioclimatic region and demonstrated lower drought tolerance. Similar patterns have been observed previously in intraspecific assessments, where populations from more arid regions exhibit greater drought tolerance (Voltas et al. 2015). These findings highlight the role of natural distribution and biogeographical affinity in determining species' ability to withstand arid conditions.

Performance of the Drought-Tolerant Tree Species

Evaluating species performance in warm and dry climates is crucial for selecting suitable candidates for afforestation in arid regions (Fuchs et al. 2021). *Eucalyptus* species not only had the highest survival rates but also exhibited the largest canopy areas and heights, reinforcing their exceptionally great drought tolerance (Schwarz et al. 2020). Although larger trees generally experience higher mortality during extreme droughts, dying at twice the rate of smaller trees (Stovall et al. 2019), this pattern did not apply to *Eucalyptus*. In contrast, *P. halepensis*, which had the largest native canopy at the end of the moderate drought phase, suffered complete mortality during the intensified drought phase. This result underscores the apparently strong water-use efficiency in *Eucalyptus*, which may stem from their ability to extract deeper water more effectively (Cavaleri et al. 2014) and access resources unavailable to native species, especially in drier conditions (Granda et al. 2022). Overall, our study provides evidence that some non-native species outperform native species (Parker et al. 2013) and that this effect can be further amplified under abiotic stress (Shabani et al. 2020).

Spontaneous Spread of Arboretum Species

Detecting emerging invasive species remains a challenge in invasion science (Fanal et al. 2021). Arboreta provide valuable opportunities to monitor the spread potential and invasion risk of non-native trees (Carrillo-Gavilan & Vila 2010; Reisman-Berman et al. 2019). At the J.U.S.T. Arboretum, five out of the 78 non-native species "escaped" and established outside the plantation area.

Among these five species, *Acacia cyclops* and *Ailanthus altissima* exhibited the greatest long-distance dispersal. *Ailanthus altissima* produces winged samaras, facilitating wind dispersal (Landenberger et al. 2014), while the bright red funicle of *A. cyclops* seeds attracts birds, aiding in dispersal and enhancing germination (Glyphis et al. 1981). *Acacia cyclops* is widely invasive in South Africa's Mediterranean-climate coastal vegetation (Morris et al. 2019); its success in resource-poor environments is likely driven by deep rooting and N_2 fixation (Morris et al. 2015, 2019), making it the most significant invasion risk among the studied species. In contrast, *A. victoriae*, *A. saligna*, and *Brachychiton populneus*, with heavier seeds lacking wind adaptations, exhibited limited dispersal. Although *Prosopis* species are global invaders (Polley et al. 2003; Muturi et al. 2013; Ravhuhali et al. 2021), including in Jordan (Alassaf et al. 2020), the species did not spread, likely due to the absence of grazing animals, which play a key role in seed dispersal and germination (Ravhuhali et al. 2021).

Impacts on Understory Biodiversity

In arid and semiarid ecosystems, tree canopies modify the microclimate by influencing soil properties, lowering temperatures, and reducing light availability (Breshears et al. 1998). While partial shade can buffer extreme temperatures, benefiting some species (Alrababah et al. 2007; Jiao et al. 2012), many arid land plants are shade-intolerant (Hunt et al. 2004; Alrababah et al. 2007; Haq et al. 2024). Indeed, we found a pronounced difference in vegetation composition in open versus canopy plots. Moreover, the effects of tree canopy systematically differ

between native and non-native species, possibly due to differences in their functional traits or ecological niches (Van Kleunen et al. 2010).

Overall, tree canopies reduced understory cover regardless of species origin. However, while canopy effects on understory biodiversity were negligible to mild for most species, non-native trees altered understory composition. *Sonchus oleraceus*, *Solanum nigrum*, and *Urospermum picroides* are common weeds associated with disturbed habitats (Al-Eisawi 1996), and were found exclusively beneath non-native canopies. This pattern suggests that non-native trees may be altering microhabitat conditions in ways that favor ruderal species. Notably, *Eucalyptus* had an exceptionally strong negative impact, consistent with ecological concerns about its biodiversity-reducing effects (Williams 2015).

Canopy structure influences shading effects, with factors such as shape, size, and leaf density playing a key role (Majasalmi & Rautiainen 2020). For example, the columnar canopy of the introduced conifer *T. articulata* had a weaker negative impact on understory diversity than the broader canopy of native *Juniperus phoenicea*. Similarly, open-canopy leguminous species like *Prosopis chilensis* and *A. farnesiana* exerted less impact than denser species such as *A. cyclops*. These findings suggest that light availability is a key factor in structuring understory plant communities (Valladares & Niinemets 2008), influencing species distribution beneath and beyond tree canopies.

Allelopathy may also influence understory diversity. Certain tree species release chemical compounds that inhibit directly seed germination or plant growth (Chaves Lobón et al. 2023) and influence understory diversity (Barbier et al. 2008). The known allelopathic impacts of *Eucalyptus* species (Chu et al. 2014) coincide with significantly reduced understory cover and diversity (Becerra et al. 2018). For example, *Eucalyptus camaldulensis* is widely used in arid afforestation due to its drought tolerance, but poses significant ecological risks due to its allelopathic traits (Reisman-Berman et al. 2019). Reduced understory cover beneath *Eucalyptus* species can accelerate soil erosion (López-Bermúdez 1990), decrease forage availability (Al-Humaid & Warrag 1998; Alrababah et al. 2007; Xu et al. 2023), and disrupt landscape connectivity (Honnay et al. 2002; Reisman-Berman et al. 2019). These findings highlight the need to exclude *Eucalyptus* species from afforestation projects aimed at preserving biodiversity, ecosystem integrity, and vital ecosystem services for local communities.

Site-Specific Considerations in Ecological Impact Assessments

The ecological impact of afforestation is highly site-dependent, influenced by local biotic and abiotic factors (Shabani et al. 2020). Afforestation outside a species' native range often alters its behavior, potentially causing habitat changes and ecological disturbances (Kaur et al. 2012; Pyšek et al. 2012). Species that are invasive elsewhere may behave differently under different environmental conditions (Rosche et al. 2019; Lucas et al. 2024) For example, while *P. juliflora* aggressively invades the Sudanian bioclimatic region of Jordan (Alassaf et al. 2020), we found that it exhibited high mortality and no spread in the arid Irano-Turanian region. Similarly, despite its global invasion risk (Henderson 2001; Dufour-Dror 2012; Reisman-Berman et al. 2019), *Eucalyptus* showed no establishment at or beyond the arboretum borders, aligning with studies indicating low spread potential at latitudes above 27°N (Rejmánek & Richardson 2011; Callaham et al. 2013).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Performance of native (blue), non-native (red), and *Eucalyptus* (dark red) tree species.
Figure S2. Effect of native (blue dots) and non-native trees (red dots) on the community composition of the herbaceous layer.
Figure S3. Total cover in the herbaceous layer plots of the arboretum.
Figure S4. Diversity of the herbaceous cover in plots under native (blue), non-native (red), and *Eucalyptus* (dark red) tree species and the control plots (gray).
Table S1. Annual precipitation and maximum temperature during the hottest months (June–September) recorded at the J.U.S.T. campus over a 24-year period (2000–2024).
Table S2. Mortality percentage of tree species planted in the Arboretum at the end of the 2009, 2019, and 2024 growing seasons.
Table S3. List of 62 understory species recorded across inside and outside canopy areas, including species found in both conditions, exclusively inside canopies, and exclusively outside canopies.

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