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Photosynthetic Characterization of Invasive Plant Diversity in Los Angeles County from 1830-2010

A thesis submitted in partial satisfaction
of the requirements of the University Honors Program
of Loyola Marymount University

by

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Abstract

The increase in atmospheric CO₂ levels due to climate change may greatly impact invasive plant species, which are non-native organisms that spread unchecked in space and negatively impact native organisms. The success of these invasives may be related to specific traits, such as their photosynthetic pathway. We acquired the specimen information for invasive species registered in the Consortium for California Herbaria of the University of California Berkeley to evaluate the community dynamics of 1,000 invasive species in Los Angeles County. We found that both diversity and richness of invasive plant species has increased over a period of 180 years. We hypothesize that the pattern of occurrence of a given photosynthetic pathway may correspond with historical increases in atmospheric CO₂ concentrations, therein favoring invasives with a C₃ photosynthetic strategy. We utilized the primary literature to identify the photosynthetic pathway for all of the invasive plant species in our database, then used curve-fitting techniques to evaluate the change in richness for C₃, C₄, and CAM. We found evidence to support that C₃ invasives were indeed favored over C₄ and CAM. We are currently examining stomatal densities of historical specimens in order to link this finding to CO₂ levels. If stomatal densities of these C₃ invasives has decreased, they have been responding to increased CO₂, supporting our hypothesis.

Introduction

Invasive species are anthropogenically-introduced, non-native organisms that aggressively expand their range across the habitats they invade and negatively impact local communities. These species threaten the integrity of agricultural and natural ecosystems throughout the world in a variety of ways (Callaway et al., 2000). Common examples include escaping natural controls (e.g. predators and herbivory), limiting local resources, altering soil stability, promoting erosion, colonizing open substrates, affecting the accumulation of leaf litter, salt, other soil macronutrients, and promoting or suppressing fire (Brooks et. al., 2004). Invasive species have enhanced performance in their introduced ranges, with larger size, more successful reproductive performance, and higher abundance (Parker et al., 2013).

Plant fitness revolves around the ability to gain carbon for growth and reproduction (Ehleringer & Monson, 1993). Plants have evolved three different pathways to uptake carbon in the form of CO₂ gas. Each process is named for the number of carbons in their first stable organic acid formed during uptake: C₃, C₄, and CAM photosynthesis. C₃ plants are the most basic pathway in which rubisco (ribulose-1,5-bisphosphate) is the main CO₂ acceptor molecule. C₄ and CAM plants evolved more specialized pathways to deal with stressful environments (Keeley & Rundel, 2003).

However, as rubisco has a high affinity for O₂ as well as CO₂, it is an inefficient method of carbon fixation (Ehleringer & Monson, 1993). When oxygen outcompetes CO₂, rubisco catalyzes photorespiration, which is an energetically unfavorable energy production pathway for plants (Keeley & Rundel, 2003). C₄ and CAM photosynthetic pathways use phosphoenolpyruvate (PEP) carboxylase to concentrate CO₂ around rubisco, thereby maximizing photosynthesis and minimizing photorespiration (Keeley & Rundel, 2003). In C₄ photosynthesis, which first evolved in grasses during periods of low atmospheric CO₂, carbon

fixation reactions are separated spatially in structures called bundle sheaths cells. Thus, C₄ plants should be favored in hot, low CO₂ environments (Sage, 2004).

CAM plants evolved in arid or quick drying and hot environments, where water availability is the most important selective pressure. CAM plants separate carbon fixation temporally, by opening the stomata during the night and closing them during the day. By only opening stomata, the structures which control CO₂ input and H₂O export, when it is cool, the plant minimizes water loss due to transpiration (Keeley & Rundel, 2003). The CAM pathway is commonly found in many succulents and epiphytes. Overall, C₃ and C₄ plants can occupy similar habitats with ecological differences occurring across seasonal and topographical gradients in temperature and moisture, while CAM plants are favored in water-limited habitats (Ehleringer & Monson, 1993).

Before the industrial revolution, atmospheric CO₂ concentrations never exceeded 280 ppm. Today, atmospheric CO₂ concentration is over 400 ppm, a level higher than at any time in the past 650,000 years (IPCC, 2007; NOAA, 2016). As a result, evaluating elevated CO₂ on plants is being addressed in multiple ways, including field study manipulations and historical data. Field studies like Free-Air CO₂ Enrichment (FACE) initiatives seek to determine the effects of elevated CO₂ on plants in completely open-air conditions (Leakey et al., 2009). FACE plots are surrounded by a ring of pipes, which release CO₂ and account for changing wind conditions to keep [CO₂] constant. FACE empirical studies have found that elevated CO₂ stimulates photosynthetic carbon gain for plants that use C₃ photosynthesis. On the other hand, elevated CO₂ does not directly stimulate C₄ photosynthesis, but can indirectly stimulate carbon gain for these plants during drought conditions (Leakey et al., 2009).

Additionally, the historical response of stomatal density and index to elevated CO₂ has been investigated (Royer, 2001). Stomatal density is a function of the size of the stomata plus the size of the epidermal cells, whereas stomatal index normalizes for the expansion of epidermal cells. Royer (2001) used three types of plant data: experimental studies (such as

FACE), pre-fossil (herbarium) samples, and fossilized leaves. The majority of the studied plants did respond inversely to elevated CO₂, validating this method for determining historical climate changes based on CO₂ concentrations. Fossilized leaves showed the most consistent inverse response in both stomatal density and index, with experimental data showing the most inconsistencies. More herbarium samples had inverse responses in their stomatal index than in their stomatal density.

In the present study, rather than seeking to reconstruct past climates, we know that atmospheric [CO₂] has increased significantly in the past 200 years and want to examine plants' response. In Royer (2001), only C₃ plants were used, because C₄ plants were thought to be physiologically insensitive to moderate CO₂ changes. We wanted to test this further by looking at responses from C₃, C₄, and CAM plants to determine if one pathway is favored in elevated CO₂ conditions. Herbarium specimens were chosen because they would allow us to study a timeline of the significantly elevated atmospheric [CO₂] in the past 200 years. Invasive species were chosen because if one photosynthetic pathway was favored, we would be able to see a selective advantage in the form of increased accumulation of invasive species with that pathway.

Our objective in this study is to use herbarium data to evaluate the change in invasive species richness and diversity over the last 200 years and characterize invasive species with respect to photosynthetic pathway in order to evaluate patterns of accumulation during the same timeline. Studying herbarium specimens may provide insights on how invasive species may respond to atmospheric [CO₂] changes. We hypothesize that invasive species with a C₃ photosynthetic pathway would be favored due to their direct dependence on atmospheric CO₂ concentrations.

Methods

Specimen Data

The Consortium for California Herbaria of the University of California Berkeley (CCH) is a gateway to information about California vascular plant specimens held by 35 participating herbaria throughout California. The metadata associated with each plant specimen includes: species name, collector, collection date, county, locality, and elevation. We obtained a data set from CCH using a database filter for “noxious weeds/invasives,” which returns specimen records as defined by the California Invasive Plant Council and the California Department of Food and Agriculture. The CCH data set was also refined to Los Angeles County. Los Angeles County was selected because of its very diverse habitats which include coastal, mountain, and desert vegetation, as well as microclimates for polar- and equatorial-facing vegetation (Schoenherr, 1992).

Photosynthetic Characterization

Each species record in the database was assigned one photosynthetic pathway: C₃, C₄, or CAM. The determinations were made using primary literature, and for species that could not be identified via primary literature, determinations were made by Dr. Philip Rundel, director of the UCLA Herbarium and Distinguished Professor of Biology.

Analyses

The change in invasive species richness per decade was evaluated using a linear regression. The change in invasive species diversity per decade was also evaluated using Shannon Diversity Indices in a linear regression. For each photosynthetic pathway, the change in number of invasive species per decade was evaluated using a curve fitting Least-Squares Fit (LSF) analysis. Three curve fitting models were chosen for the LSF evaluations: linear, exponential, and logarithmic. The relationship between the model data and our data was empirically assessed using a Spearman-Rank correlation.

Results

The database of invasive species in Los Angeles County included 995 species and 13,961 individuals, collected between 1826 and 2010. The photosynthetic pathway for 486 species was identified using primary literature sources. The pathway of the remaining 509 species was determined by Philip Rundel (pers. comm.). The resulting database of LA County invasive species consisted of 12,233 C₃ species (87.6%), 1,565 C₄ species (11.2%), and 163 CAM species (1.2%).

Both invasive species richness and invasive species diversity indices showed a linear increase between 1850 and 2010. Invasive species richness increased at a rate of 2.4 species per decade ($P < 0.001$, Figure 1). The diversity index of invasive species increased at a rate of 0.02 units (H-value) per decade ($P < 0.001$, Figure 1).

The species richness of each photosynthetic pathway showed differing patterns of increase (Table 1). Invasive C₃ species correlated with a linear-fit model (Figure 3), invasive C₄ species correlated with a logarithmic-fit model (Figure 4), and invasive CAM species correlated with an exponential-fit model (Figure 5).

Discussion

Both the richness and diversity of invasives species in Los Angeles County increased between 1820 and 2000. During this 180-year timeline, approximately 2-3 exotic species invaded LA County every 10 years. The combined increase in both richness and diversity suggests that equitability among invasive species also increased, such that once an invasive species is established in LA County, its relative abundance also increases.

Categorization and statistical analysis has shown that the richness of C₃, C₄ and CAM species have each increased, but following different growth patterns. Invasive C₃ species have increased linearly, suggesting that they will continue to accumulate in LA County at a steady rate. Invasive C₄ species have increased logarithmically, suggesting that arrival is slowing as

they reach an asymptotic maximum. Invasive CAM species show exponential increase, but because they only represent 1.2% of the specimens evaluated, we believe it is too small to analyze the trend at this stage of invasion. Based on the LSF models, we propose that species invasions by C₃ species have been favored in LA County during the last 180 years, more so than invasive C₄ and CAM species.

The implication of these results for invasive species biology is that evaluations of their performance in new ranges should include photosynthetic advantages. When examining invasive species abundance and reproductive performance, the photosynthetic pathway will play an important role in how strongly these parameters increase. We propose that C₃ invasive species are favored because the C₃ photosynthetic pathway has the most direct dependence on atmospheric levels of CO₂, which increased 200 ppm during our timeline. This agrees with previous studies, which have found C₃ plants to be more responsive to CO₂ in both experimental and historical conditions (Leakey, et al., 2009; Royer, 2001).

Looking at these differing patterns of accumulation based on photosynthetic pathway demonstrates the importance of studying how changes in [CO₂] impact plant communities in pre-fossil data. As atmospheric CO₂ concentrations increase, a hypothesis that needs to be tested is if species are becoming more invasive due to their selective advantage. Additionally, it is likely that invasive species are not the only plants that exhibit this response. C₃ species of all kinds may have a selective advantage, which could drastically change ecological dynamics of plant communities as atmospheric CO₂ concentrations continue to increase.

That being said, it may not be all C₃ species or all C₃ invasives that are accumulating due to a response to elevated CO₂. The next step in our analysis is to examine the change in stomatal density and stomatal index of the C₃ species in our dataset. Determining which types of plants are showing a decrease in stomatal density and index will more strongly link the observed selective advantage with changes in [CO₂].

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Figures & Tables

Table 1. Correlation coefficient (*r*) values for LSF models (*P<0.001).

	Linear Model	Logarithmic Model	Exponential Model
Invasive C ₃ species	0.9397*	0.9367	0.8899
Invasive C ₄ species	0.8358	0.8361*	0.8349
Invasive CAM species	0.8119	0.809	0.8705*

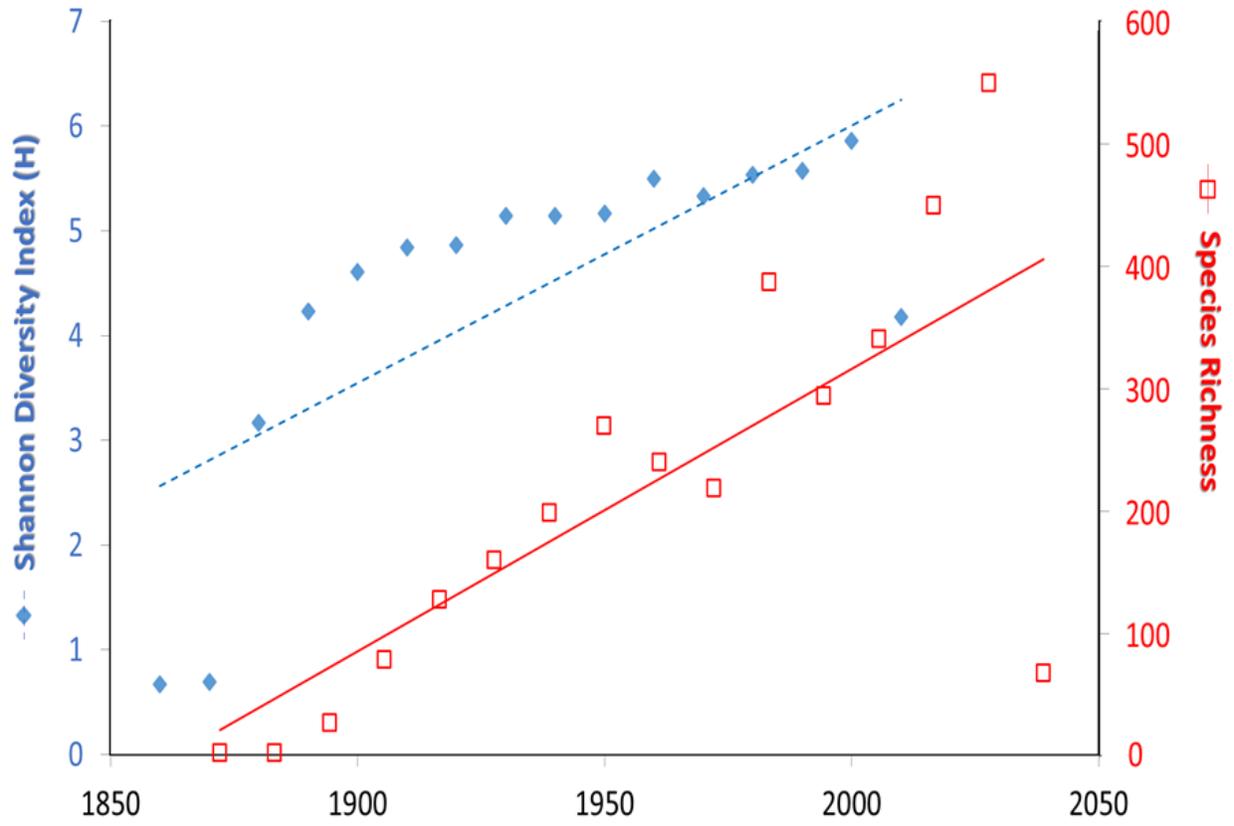


Figure 1. Change in richness and diversity of invasives in LA County, California.

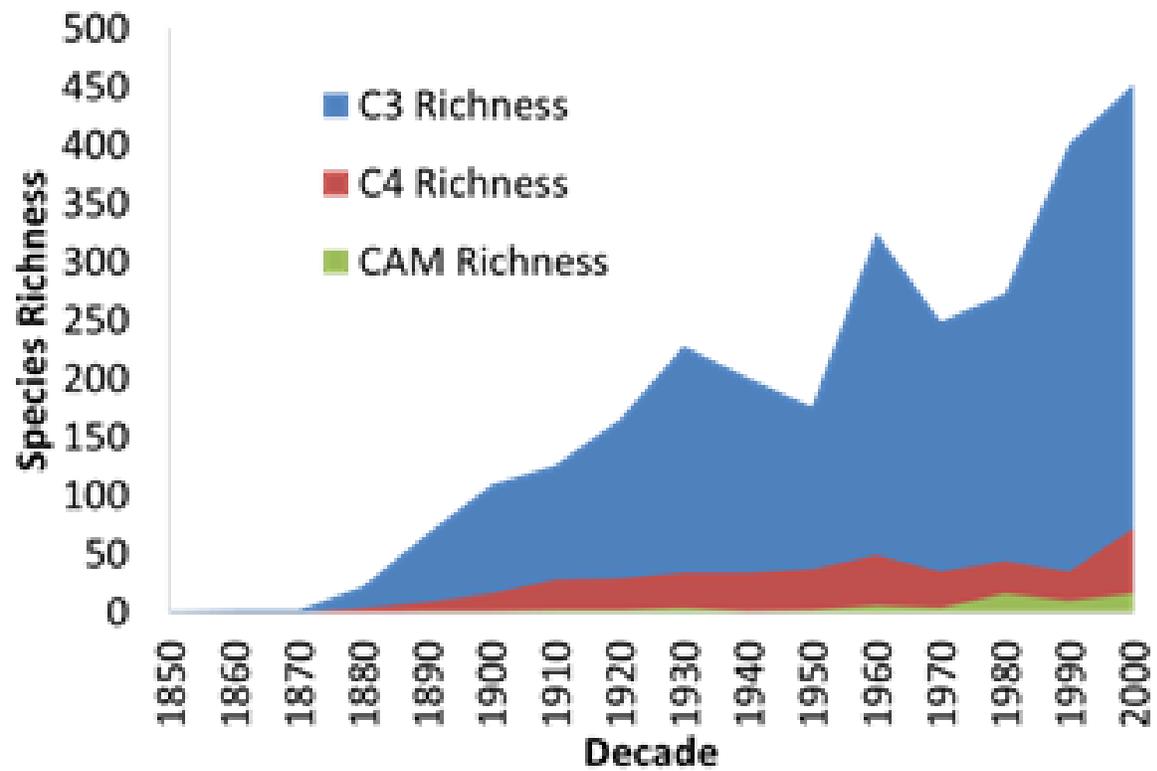


Figure 2. Proportions of C₃, C₄, and CAM species richness.

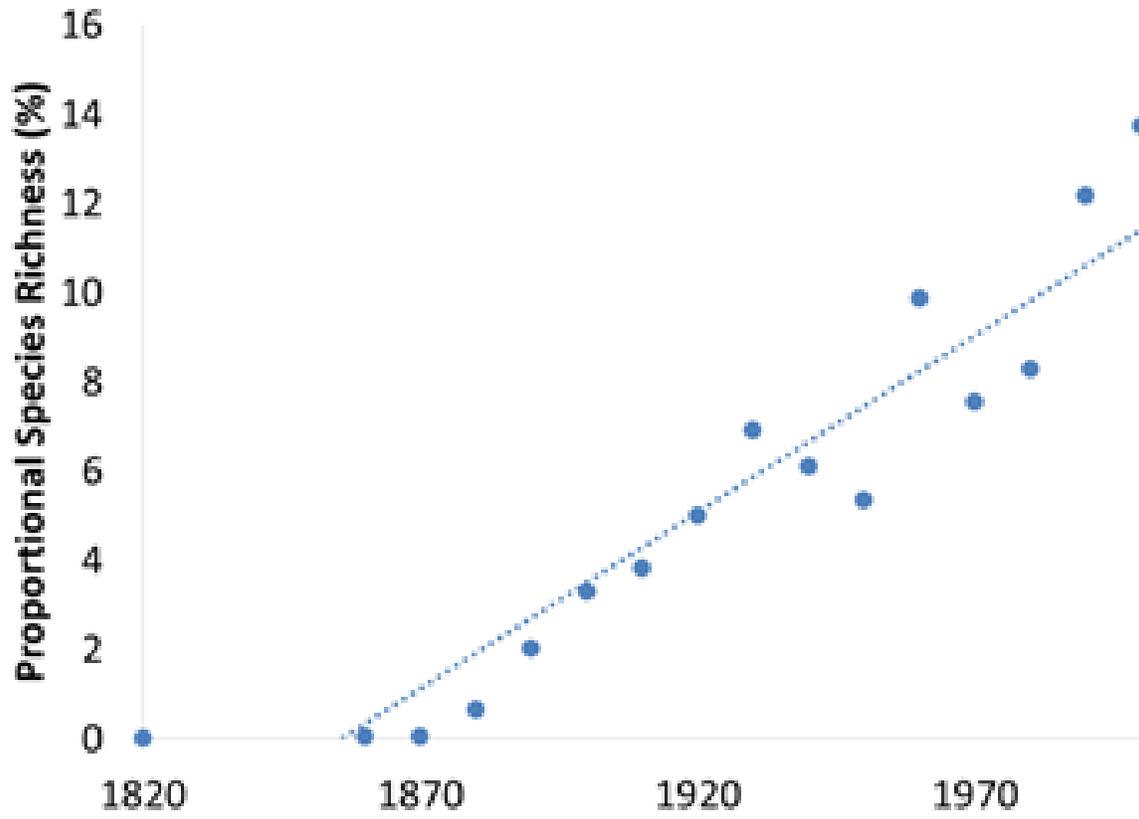


Figure 3. Linear fit of C₃ invasive species richness.

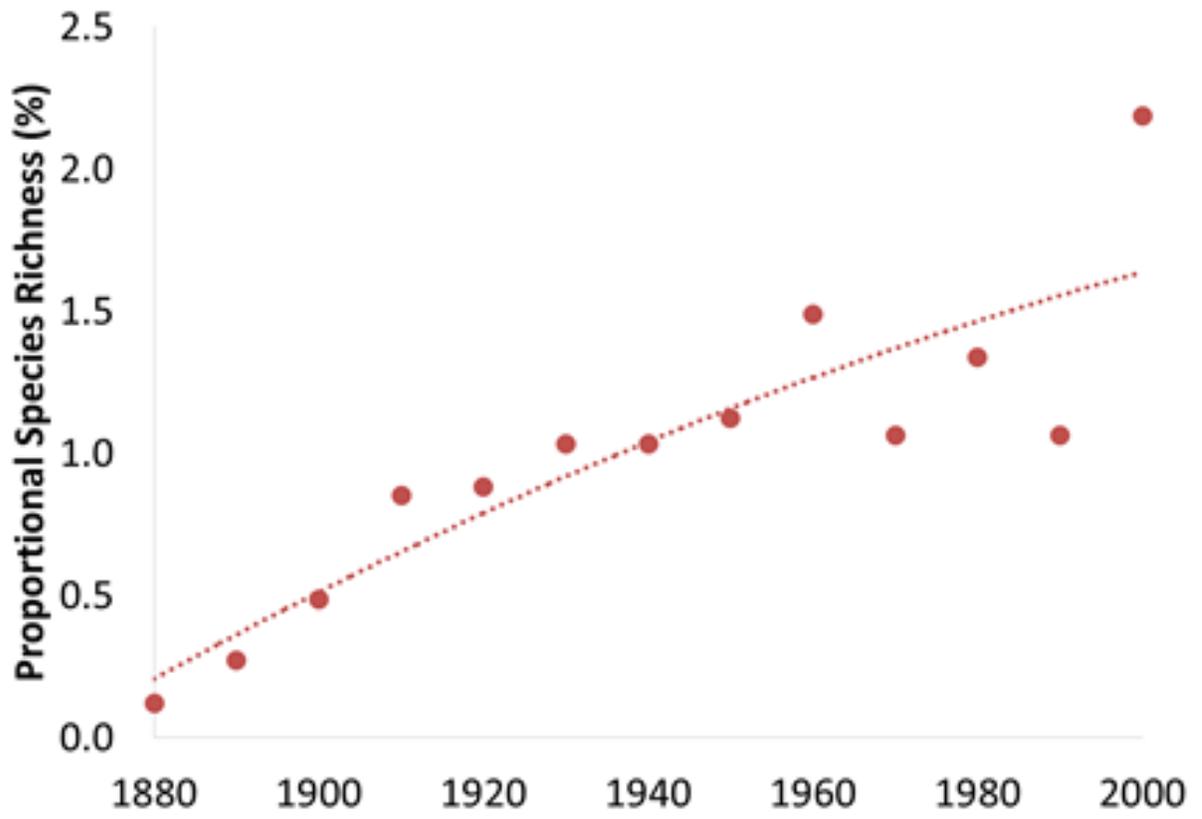


Figure 4. Logarithmic fit of C₄ invasive species richness.

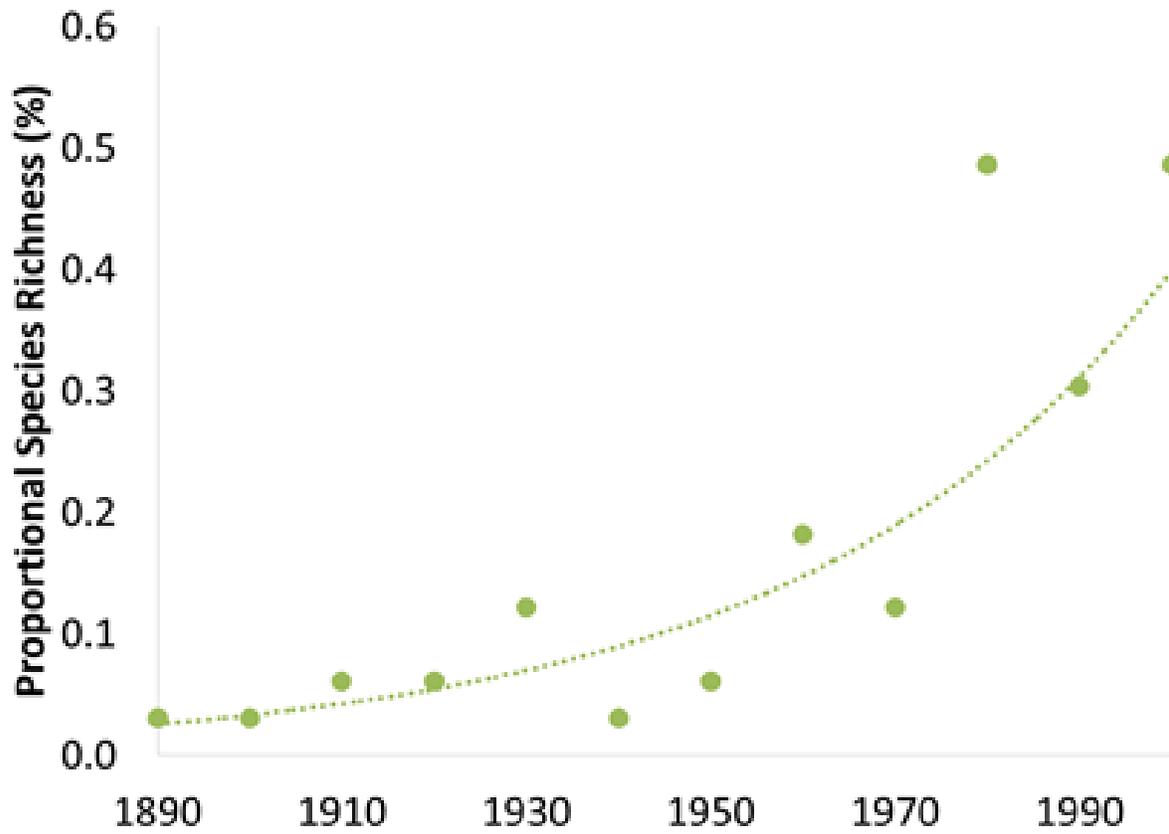


Figure 5. Exponential fit of CAM invasive species richness.