

Successional Pathways in Disturbed Chaparral: Plant Species Evidence for Primary Succession

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Abstract

In 1996, the construction excavation of a mature chaparral area at Flintridge Sacred Heart Academy created a barren area named the Cut, stripped of previously present plants, nutrients, organic matter, and soil. Thirty years later, this area is slowly redeveloping and appears to be a stable community surrounded by chaparral and coastal sage scrub. Previous studies suggest that severely disturbed areas of chaparral will not recover through either auto-succession or primary and secondary succession. Instead, the disturbed area was expected to transition to a mature coastal sage scrub community and eventually revert to chaparral via encroachment. Through an in-depth survey of the plants in our designated cut, ecotone, and chaparral areas, as well as evaluation of root depth and biodiversity calculations, the cut was compared with the surrounding mature chaparral ecosystem. Key findings include evidence that: the cut has not disclimaxed as coastal sage scrub, the ecotone is static (i.e. there is no encroachment), and soil depth is a critical factor in species selection. This study confirms that chaparral ecosystems can return from a severe disturbance through primary succession and creates an entirely new model of succession for chaparral.

1.0 Introduction

Urban expansion has caused a loss of 50% species richness worldwide, based on localized site surveys (Li et al., 2022). This threat of urban expansion extends to California's beautiful native chaparral which covers approximately six percent of the state (Syphard et al. 2018). Chaparral is a major contributor to the species richness of California and is home to 24% of California's native plant populations (Halsey & Keeley, 2016). It is also vital for reducing erosion during heavy rain through its deep root system (Rundel, 2018). Though vital, chaparral is declining due to increasing urban development. Understanding how chaparral responds to disturbance is important for maintaining this vital ecosystem of California.

1.1 History of the Area

In 1995 Crane Field was added to Flintridge Sacred Heart Academy. The land seen in 1994 of Figure I was excavated with the soil and rock used to build Crane field. A flat barren area was left over, which today is sparse in plant species and what is classified as the **cut**

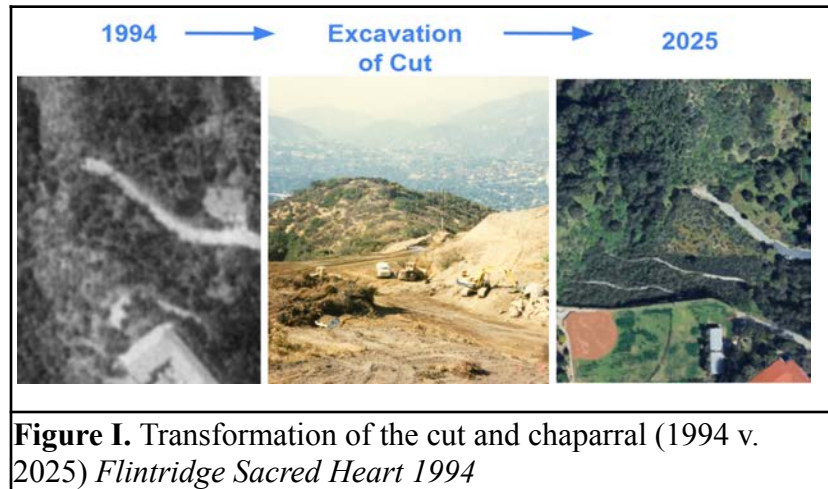


Figure I. Transformation of the cut and chaparral (1994 v. 2025) *Flintridge Sacred Heart 1994*

throughout our experiment. This disturbed area is compared to the chaparral ecosystem surrounding this area, which has been classified as **chaparral** throughout our experiment. A comparison of the studied cut and chaparral before and after the excavation is seen in The Chaparral and The Cut (1994) (Figure II) and The Chaparral and the Cut (2025) (Figure III) (Google, 1994, 2025, *Flintridge Sacred Heart Academy view*).

1.2. Classical Plant Succession Overview

Ecological succession describes how species and habitats in a terrestrial ecosystem change over time. Primary succession describes the changes from a starting point of barren land, while secondary succession occurs after a major disturbance. The most significant difference between the two succession categories is in the starting soil; secondary succession begins with soils that have previously existed with plants and seeds, while primary succession begins with barren, uninhabited land. Both primary and secondary succession follow three stages: pioneer species, intermediate species, and climax community. Pioneer and intermediate species replace each other as vegetation alters the environment, enabling new species to thrive until a stable climax

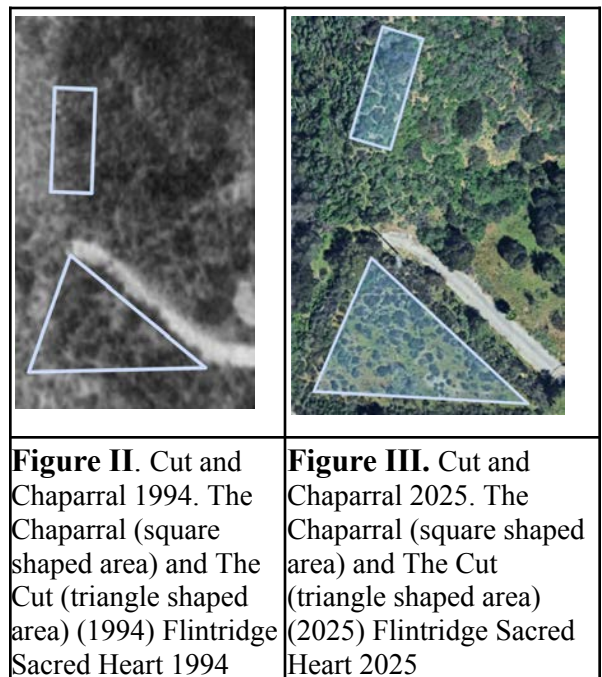


Figure II. Cut and Chaparral 1994. The Chaparral (square shaped area) and The Cut (triangle shaped area) (1994) Flintridge Sacred Heart 1994

Figure III. Cut and Chaparral 2025. The Chaparral (square shaped area) and The Cut (triangle shaped area) (2025) Flintridge Sacred Heart 2025

community forms. In primary succession, mosses and lichens colonize barren land, breaking down rock into soil. In secondary succession, grasses and perennials grow in pre-existing soil after disturbance. Intermediate species—such as grasses, shrubs, and pines—follow in both types. Climax communities are the final, stable stage, persisting for centuries unless disrupted. While both types of succession take time, secondary succession reaches the climax stage more quickly due to the presence of existing soil.

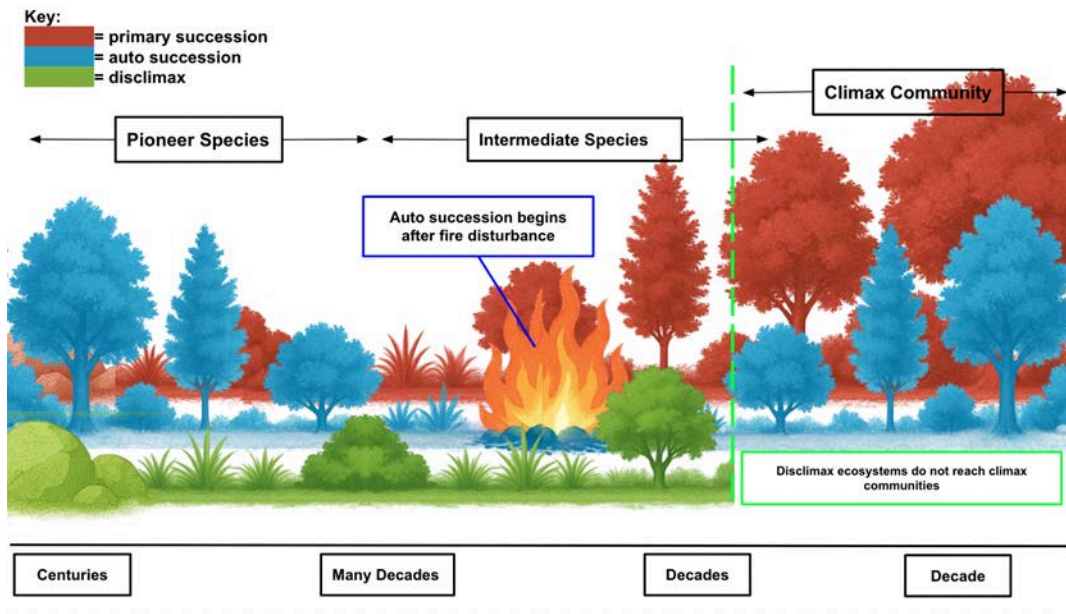


Figure IV Successional Pathways

1.3 Chaparral Characteristics - Overview of Biome, Auto Succession and Fire

The Mediterranean-type climate—characterized by hot, dry summers and cooler, wetter winters—includes both chaparral and coastal sage scrub communities (One Earth, 2016). This climate is also found near the Mediterranean Sea, central Chile, South Africa's Cape region, southwestern and southern Australia, oak woodlands, montane conifer forests, riparian woodlands, grasslands, salt marshes, and in southern California and northern Baja California (Beyers & Wirtz, 1997). Chaparral shrubs have small, tough, evergreen leaves with a waxy coating that reduces water loss (Halsey & Keeley, 2016). During summer and early autumn, fires frequently occur in the chaparral biome. While a burned area with an intact soil base might suggest secondary succession, classical plant succession does not typically occur in chaparral unless mixed with other vegetation types, forming ecotones. Instead, chaparral follows an auto-succession pattern, where fire-resistant, native chaparral species re-establish dominance

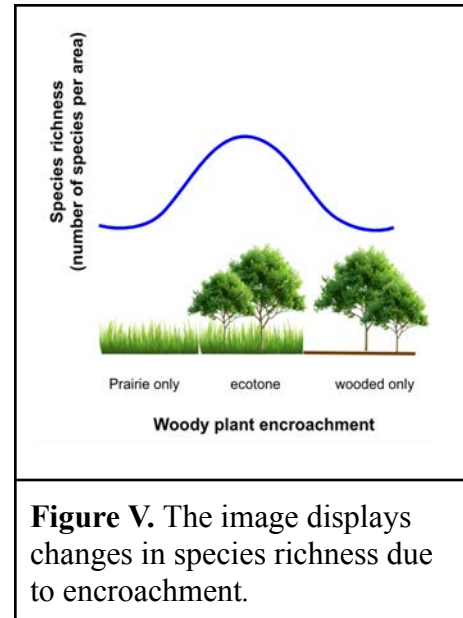
after disturbance (Hanes, 1971). A defining feature of this process is the rapid regeneration after fire. Temporary cover appears within a year, consisting of four vegetation categories—generalized herbaceous perennials, generalized annuals, specialized fire-annuals, and specialized fire-perennials—two of which are present both before and after fire (Keeley S.C., Keeley J.E., Hutchinson, and Johnson, 1981).

1.4 Coastal Sage Scrub and Disclimax in Chaparral

The coastal sage scrub (CSS) ecosystem is a distinctive plant and animal community that naturally occurs along California's coastline to Baja California, Mexico (Ellis, 2018). CSS plants feature light-colored leaves that help reflect heat, along with deep root systems that extend into soil for water access. The Environmental Studies department at De Anza College characterizes coastal sage scrub vegetation by its low-growing, aromatic shrubs. Coastal sage scrub vegetation tends to have thinner leaves that are less adapted to extreme drought and heat than those of chaparral communities. This ecosystem thrives in areas with a Mediterranean climate — hot, dry summers and mild, wet winters. In terms of disturbances, the NatureServe Explorer guide by Comer et al. explains that coastal sage scrub is not an ecosystem that depends on fire for the regeneration of its major species of shrub. It normally occupies areas cleared by landslides, debris flow, and other mass-wasting events. After a disturbance, it can temporarily occupy chaparral sites as the chaparral ecosystem turns into a disclimax (Vogl, 1952). Disclimax is a type of ecological community that remains stable over time but is not the climax community that would naturally develop in that area under undisturbed conditions. Instead, it's maintained by disturbances often caused by human activities. Eventually, the coastal sage scrub disclimax community will return to chaparral through encroachment so long as the disturbed area is not irreversibly damaged (Vogl, 1952)

1.5 Plant Encroachment

Encroachment is a different way to replace species than succession. Encroachment is a disruptive process where one climax community encroaches on another climax community or urban development encroaches on a climax community (Van Auken & Bush, 2017). During encroachment, seeds are dispersed from the invading plant community into the adjacent one, facilitated by their close proximity; this is called autochory seed dispersal. An example of encroachment is seen in Figure V with the woodland habitat and grassland habitat. During woodland plant encroachment, the grassland habitat (treeless area) becomes wooded. As encroachment happens within a specific area, biodiversity levels and species richness peaks in the ecotone (with the presence of both ecosystems as one encroaches on the other) (Van Auken & Bush, 2017).



1.6 Literature Review

Understanding Chaparral Succession- Why the Chaparral is Different

Richard Vogl presented a manuscript at a conference in 1971 that highlights a new way of thinking about chaparral and the unique chaparral succession by delving into the chaparral characteristics. After a severe disturbance chaparral will convert to a disclimax, dominated by coastal sage scrub. Additionally, Vogl suggests that this disclimax area now representing coastal sage scrub will eventually return to chaparral through encroachment as long as the disturbed land is not irreversibly damaged. This process creates an ecotone (a region that has two different biological communities, in this case, two different vegetation types). Along the ecotone, chaparral succession involving a step-wise replacement of species will occur as chaparral integrates with other vegetation types. If step-wise replacement is not occurring, then disturbed chaparral can also go through primary succession by climax chaparral species directly invading the area rather than the sequential steps of classical plant succession.

Vogl's observations suggest that after a disturbance chaparral will not go through the steps of classical plant succession and instead will disclimax and eventually return to chaparral

through encroachment. Understanding how chaparral goes through succession differently compared to other ecosystems can help interpret ecological survey data in a disturbed chaparral ecosystem compared to mature chaparral vegetation.

Pioneer Species

Dalling presents an overview of pioneer species and their role in primary succession. After a disturbance, a seed bank is accumulated in the soil from wind, gravity, or animals carrying them. Once left on the surface of the soil, they sit until germination. Pioneer species go through their life cycle quickly and die after a few years. Due to the lack of nutrients in soil when primary succession is occurring, pioneers are usually nitrogen-fixing. Dalling explained an example with the eruption of Mt. St Helens, which saw the spread of the perennial Lupine after the eruption. The Lupine (*Lupinus*) greatly increased nitrogen levels in the soil, facilitating the growth of other plant species.

Dalling highlights the important role of pioneer species in classical plant succession. After a severe disturbance, pioneer species set the stage for intermediate species and eventually climax species by returning key nutrients to disturbed soil void of nutrients.

1.7 Driving Question and Project Statement

A southern California native chaparral community at FSHA was excavated in 1997 to provide for the construction of an athletic field (Crane field). After construction, an excavated area surrounded by chaparral and oak woodlands remained. Today, nearly thirty years later, the once excavated land appears to be a stable community surrounded by chaparral and coastal sage scrub. Using this local event and subsequent succession as a model, we seek to understand the successional pathway of severely disturbed land surrounded by chaparral and oak woodlands. To address this question, an ecological survey was implemented, including both plant species and soil characteristics, which compared an area of disturbance and adjacent mature chaparral. The focus of this paper is to analyze the plant species data, while the soil data is being studied by other members of our group (Dunn & Pangilinan). There are three successional pathway options for this disturbed area: Disclimax, primary succession, secondary/auto succession.

State	Hypothesis and predictions
If the disturbed area is returning to chaparral through the successional pathway of disclimax...	Then coastal sage scrub species should dominate the disturbed area.
If the disturbed area is undergoing primary succession...	Then chaparral pioneer species should solely exist in the disturbed area compared to the chaparral.
If the disturbed area is undergoing secondary succession/auto succession...	Then the disturbed area should share a nearly identical community of plants compared to the chaparral.

2.0 Methods

2.1 Interrupted Belt Transect

Three surveys of perennials and annuals were performed using an interrupted belt transect.

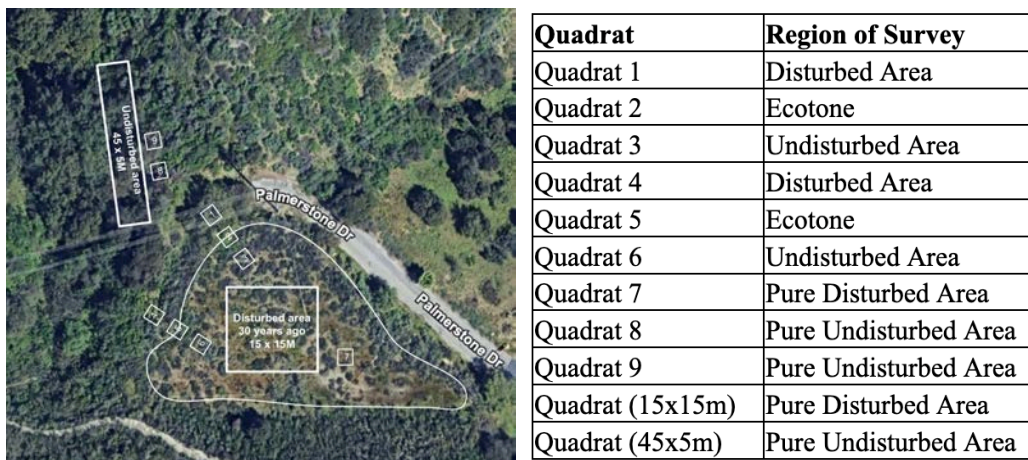


Figure VI. Visual Representation of Surveyed Area and Quadrant Key

Surveys for quadrats 1, 2, and 3 established a gradient from the disturbed area (cut), through the ecotone, to the undisturbed area (chaparral). A quadrat (three meters by three meters) was randomly chosen for areas within the cut, the Ecotone, and the chaparral. The setup was repeated for a survey of quadrats 4, 5, and 6.

A survey of quadrat 7 evaluated plants in the purely disturbed area, while quadrats 8 and 9 represented the purely undisturbed area.

A final survey evaluated plants on a grander scale to compare the cut and the chaparral. A quadrat (fifteen meters by fifteen meters) was randomly selected within the disturbed area, and a quadrat (five meters by forty-five meters) was selected for ease of access – for reasons of similar

sun exposure and the presence of bedrock near the surface – within the undisturbed area. This survey only evaluated perennials.

2.2 Quadrat Biodiversity

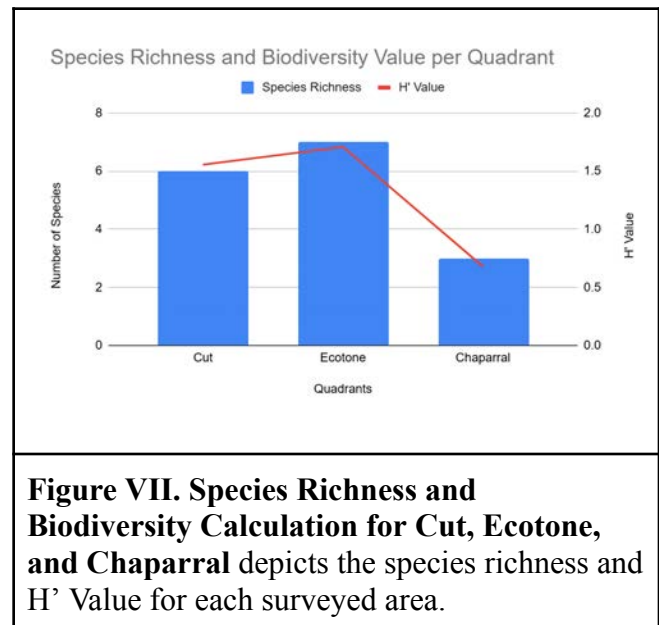
The plant biodiversity of each quadrat was evaluated on an evenness and richness scale. Plants were counted by the number of variations of plant species (species richness) and the abundance of each species type (species evenness). Species evenness was used to create a species-area curve and ensure sufficient sampling. Plant species were identified using three sources guided by experts in plant identification and using *iNaturalist*, *Pl@ntNet Identify*, and *Nature Collective*. Plant biodiversity was calculated using the Shannon-Weiner Diversity Index (Appendix - Figure XI). The full experimental methodology is found in Appendix 7.1.

3.0 Results

3.1 Species Richness and Shannon-Weiner Diversity Index

Figure VII displays the species richness with the biodiversity value layered on top. The surveyed species richness of the cut (quadrants 1 and 4), the ecotone (quadrants 2 and 5), and chaparral (quadrants 3 and 6) indicates that the ecotone had the highest species richness compared to the cut and chaparral. The layered Shannon-Weiner Diversity index mirrors the richness graph with the largest H' value at the ecotone. This survey encapsulates an accurate overall view of the ecosystem due to the results from the calculated species area curve in Appendix 7.2.

3.2 Species Evenness of Perennials



The surveyed species evenness of all perennial species was performed in one quadrat (measuring fifteen meters by fifteen meters) of pure cut and one quadrat (measuring forty-five meters by five meters) of pure chaparral. The term “pure” means the quadrants surveyed were completely removed from the ecotone. The overall distribution of

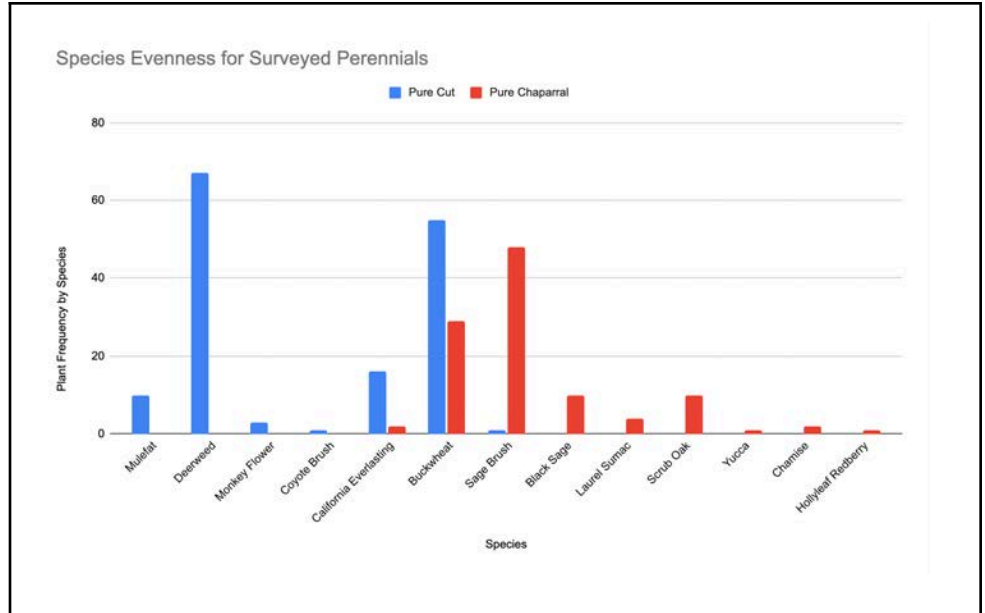


Figure VIII. Species Evenness for Perennials of Cut and Chaparral

evenness shown in Figure VIII indicates that there is a clear group of species that belong to the cut and the chaparral, with one notably overlapping species: buckwheat. This survey encapsulates an accurate overall view of the ecosystem due to the results from the calculated species area curve in Appendix 7.2.

3.3 Average Root Depth of Surveyed Species

Figure IX displays the root depth of surveyed perennial plant species in a cut quadrat (measuring fifteen meters by fifteen meters) and chaparral quadrat (measuring forty-five meters by five meters). Notice that the root depth of plants in pure chaparral has a distinctively deeper root system. (Nature Collective).

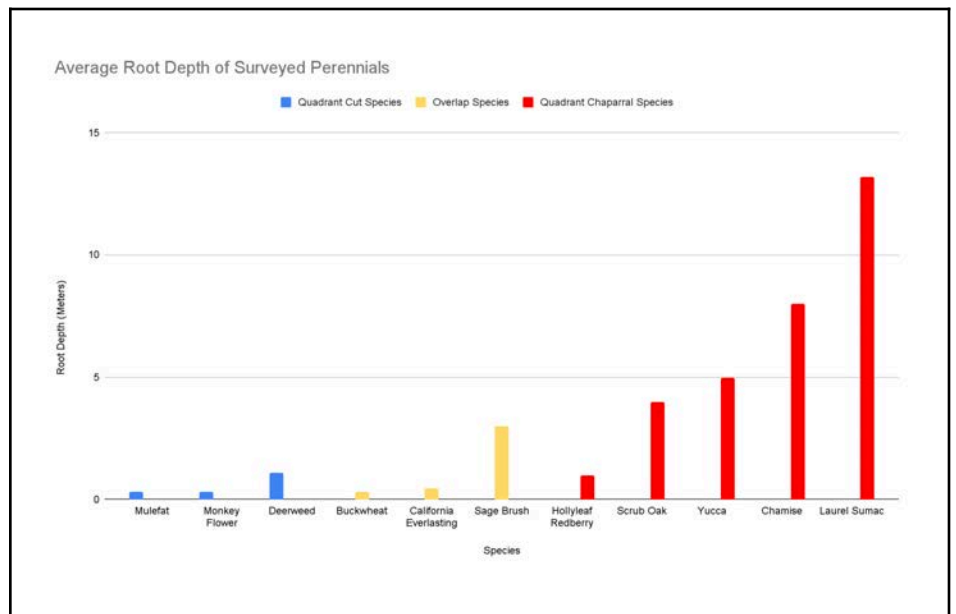


Figure IX. Average Root Depth of Surveyed Species

4.0 Discussion

After a severe disturbance in chaparral, Vogl would expect the area to go through primary succession, then disclimax to an ecosystem representing coastal sage scrub. The surveys indicated that the community on the cut was not a

mature Coastal Sage Scrub community due to the lack of climax coastal sage scrub species, negating a disclimax as the successional pathway.

Vogl believed that if the disturbed area wasn't irreversibly damaged, it would eventually become a coastal sage scrub disclimax community

State	Hypothesis and predictions	Results
If the disturbed area is returning to chaparral through the successional pathway of disclimax...	Then coastal sage scrub species should dominate the disturbed area.	Disclimax result: A disclimax is not happening because coastal sage scrub is not dominating the area nor inhabiting the soil.
If the disturbed area is undergoing primary succession...	Then chaparral pioneer species should solely exist in the disturbed area compared to the chaparral.	Primary succession result: Primary succession is occurring because chaparral-specific pioneer species are slowly emerging in the area.
If the disturbed area is undergoing secondary succession/auto succession...	Then the disturbed area should share a nearly identical community of plants compared to the chaparral.	Secondary succession/ auto succession result: Because the plant community is primary chaparral with minimal diversity (i.e. few variations of coastal sage scrub and other species), neither secondary- nor auto succession is occurring.

Figure X. Hypotheses and their results

and would experience a gradual transition to chaparral by encroachment, which happens along an ecotone. The Species Richness and Biodiversity Calculation for Cut, Ecotone, and Chaparral (Figure VII) shows a higher value of different species and biodiversity in the transition between the cut and the chaparral (i.e. an ecotone). The ecotone is precisely centered on the original cut boundary, indicating that it has been static over decades. Additionally, encroachment is one stable ecosystem invading another. The ecosystem in the cut is a pioneer community, so encroachment is not possible by definition. Moreover, these pioneer species are present throughout the cut and not just expanding inwards from the ecotone, confirming succession is happening independently of the ecotone via non-autochory seed dispersal.

The lack of coastal sage scrub keystone species and the static ecotone suggests that disclimax to encroachment is not the current successional pathway and the data shows evidence of what may be preventing this pathway. The Average Root Depth of Surveyed Species (Figure IX) demonstrates that species in the cut typically have roots that don't run deeper than the

topsoil. When collecting soil samples from the pure cut quadrant, bedrock was encountered within the first five centimeters, indicating very shallow soil depth. This may be a critical factor in the type and pace of succession that is occurring in the cut. The lack of depth in the soil may be preventing disclimax as mature coastal sage scrub plants with deep root systems cannot physically live there and also prevents chaparral climax species from encroaching for the same reasons (see Hypothesis and their results Figure X). Overall, the data confirms that Vogl's expectation of disclimax is not happening, and the assumption that this is the only successional pathway for chaparral may be an oversimplification. The sister group to this study (Pangilinan and Dunn), who analyzed the successional pathways through soil data, has reached the same conclusion. A comparison of soil properties: texture, organic matter content, and pH between the areas surveyed indicates that while soil development is slow, ecological recovery is happening.

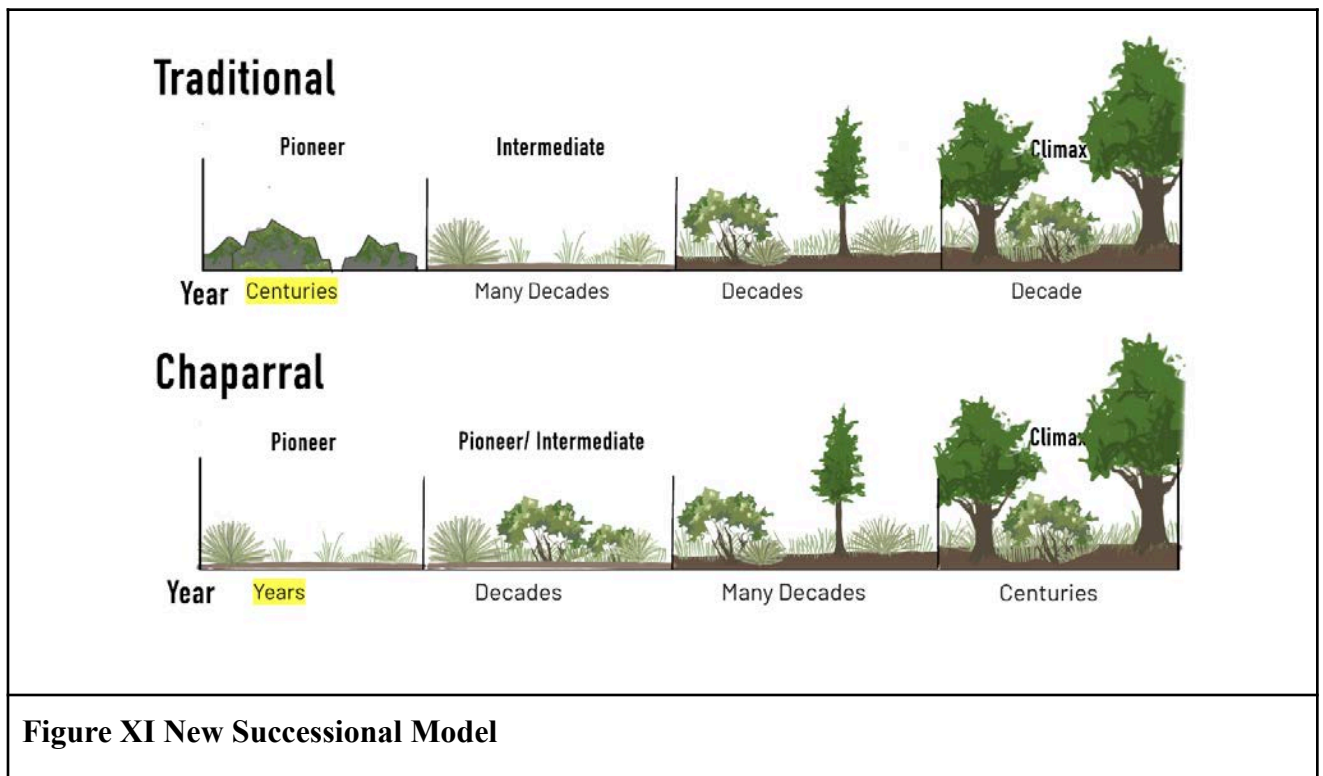
Two larger, perennial species, surveys indicate the cut is undergoing the initial stage of secondary succession. Perennials are indicators of the succession stage of a chaparral ecosystem because they include chaparral pioneer species and chaparral climax community species. Species Evenness for Perennials of Cut and Chaparral (Figure VIII) provides three key pieces of evidence supporting this claim. First, a population of pioneer species, Deerweed (*Acmispon glaber*) and Coyotebrush (*Baccharis pilularis*), only found in the cut, is present, aligning with our hypothesis. Dalling explained in 2008 that pioneer species are essential because they are nitrogen-fixing plants that aid in returning key nutrients into the soil and set the stage for the growth of intermediate species. Deerweed and Coyotebrush are both nitrogen-fixing plants, meaning they are playing an important role in returning key nutrients into the soil for later chaparral climax species. Pioneer species, as Dalling explained, have a short life span as intermediate species replace them. Their significant population in the cut suggests that primary succession is happening very slowly.

Intermediate species such as Buckwheat (*Eriogonum fasciculatum*), California everlasting (*Pseudognaphalium californicum*), and Sagebrush (*Artemisia tridentata*) are found both in the cut and in the chaparral, indicating that the cut is developing into an intermediate succession stage.

Climax species (Laurel sumac (*Malosma laurina*), scrub oak (*Quercus berberidifolia*), Chamise (*Adenostoma fasciculatum*), and Hollyleaf redberry (*Rhamnus ilicifolia*)) are found exclusively in the chaparral, confirming it as a mature community. Their absence in the cut

suggests it has not yet reached the final stage of succession. Based on this species distribution, we observe a clear pattern of successional stages across zones: pioneer and intermediate species in the cut, and intermediate and climax species in the chaparral, indicating primary succession is occurring.

Secondary succession/auto-succession is not evident from the data, but the presence of intermediate species may indicate a transition to secondary succession. Species Evenness for Perennials of Cut and Chaparral (Figure VIII) shows that between the cut and the chaparral, there is an overlap of only three species, indicating that secondary succession has not occurred. However, the overlap of these three species also indicates that the soil composition between the cut and chaparral is starting to become similar and can support the same species. Due to the drastic change in the soil depth between the surveyed areas, this most likely means the depth in the cut has expanded enough to support more chaparral species, potentially the beginning of secondary succession.



The timeline for traditional primary succession suggests that it will take centuries for pioneer species to establish themselves in a disturbed area. And from then on the intermediate stages and climax stages of primary succession will take decades. This primary succession model is said to

be applicable to all ecosystems. However, through our results we were able to create an entirely new successional model unique to chaparral. Our new model is reversed, in that the primary stage takes years instead of centuries which progresses into decades and then centuries.

A future follow-up study investigating slowly developing areas similar to the cut sampled for this experiment would verify this result. For example, an evaluation of the freeway cuts showing first stages of growth and sprouting could provide confirmation. Another important assessment is the timeline this study may follow. Within the span of thirty years, approximately three centimeters of organic soil developed above the clay layer all throughout the cut. Full recovery of the cut may take centuries, and understanding the minimum soil depth for mature chaparral to develop provides insight into the successional pathway of such an ecosystem; it is the key to supporting climax chaparral in its full capacity.

5.0 Conclusion

A severely degraded area, the cut, near Flintridge Sacred Heart Academy, provided a unique opportunity to study chaparral succession over a decades-long interval. The published theories of chaparral succession, particularly those of Vogl, suggested an expected state of the plant community on the cut and a plant succession model that differs from classical models. The FSHA survey data – evaluating plant biodiversity, root depth, and soil characteristics – indicate that classical primary and secondary succession do occur in chaparral communities, but the process occurs over very long timescales (decades to centuries) and doesn't involve encroachment. The data support another of Vogl's assertions in that a local factor, soil depth, is limiting the pace of succession. Since soil depth will typically be shallow in cases of severe degradation, this is a critical driver of the pace of chaparral succession. These findings provide valuable insights into how chaparral succession occurs on severely degraded sites that are valuable to experts working in chaparral restoration projects.

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7.0 Appendix

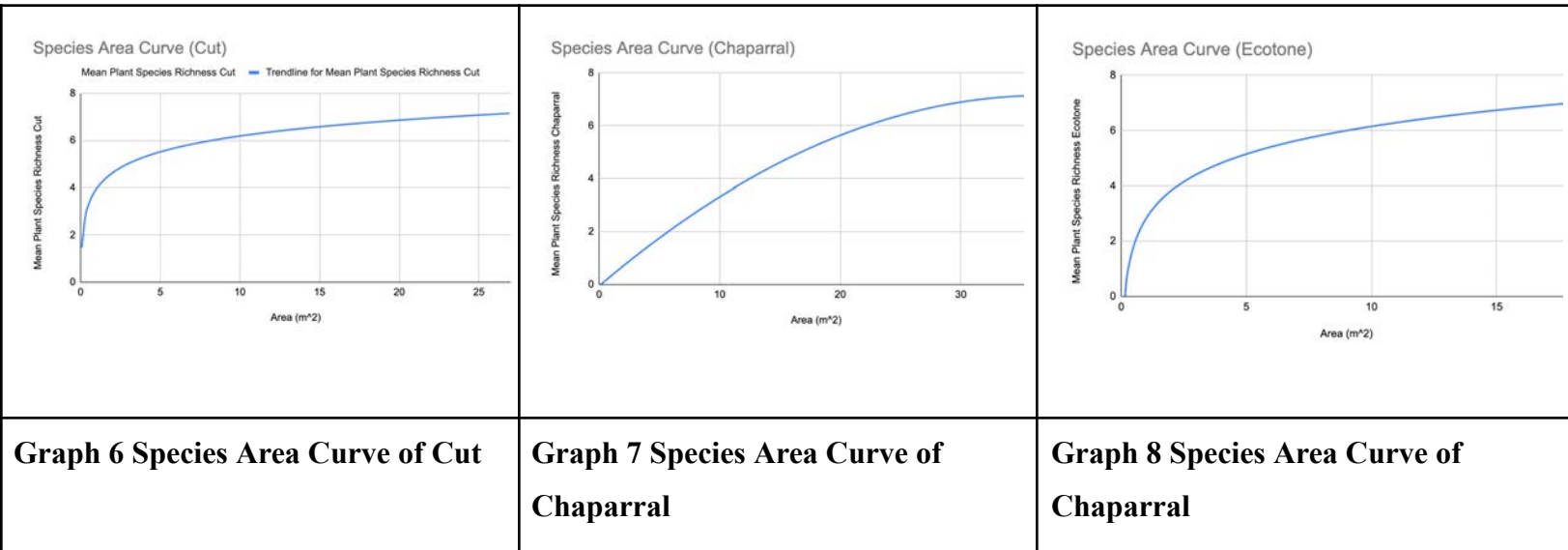
7.1 Shannon-Weiner Diversity Index

The diversity index is evaluated using factors of evenness and richness (figure X). P refers to species evenness. A larger value of H' indicates larger biodiversity. Evenness and biodiversity have a direct relationship. Low to moderately high values of biodiversity range from 0.3-1.5. High biodiversity values range from 1.6 and above

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

Figure XI Shannon Weiner Diversity Index.

7.2 Species Area Curve



Graphs 6, 7, and 8: Overall Species Area Curve and Species Area Curves of Cut and Chaparral

The species area curve demonstrates that as the cumulative area of the survey of the site increases, the number of species recorded begins to increase and then plateau. (University of Minnesota Duluth) Reaching the plateau shows you have sampled the majority of species present in that community because it demonstrates no new species are being added to the richness as the curve is not increasing. The species-area curve plots the average number of species detected (y-axis) against the cumulative area sampled (x-axis). It is noticeable that both graphs are plateauing showing an accurate survey.