- Objectives:
  - How can the foundations of and theory in community ecology ↔ restoration ecology ↔ ecological restoration?
    - Disturbances and Succession
      - Key concepts to understanding and restoring ecological systems
        - » Types, intervals, severity, etc. of disturbance
        - » Natural vs. anthropogenic disturbance
      - Can restoration be accelerated by manipulating disturbances and/or succession?
        - » Eliminating unnatural vs. restoring natural disturbances
        - » Can we fast-forward succession in ecological restoration?
    - Multiple states and restoration trajectories
      - Targeting the ever-changing nature of ecological systems

- What is ecological succession?
  - Directional change in species composition, structure, and resource availability over time that is driven by biotic activity and interactions, and changes in the physical environment



 1° Succession (no soil or plant propagules on site) following glacier retreat



• 2° Succession (at least some soil and propagules on site) in old fields (i.e., old field succession)







• Models of succession (older)



(Barbour *et al*. 1999)

- Models of succession (newer)
  - As resource supply changes, communities change
    - Mechanistic Disturbance, stress & competitive interactions as selective forces



Tilman's Resource-ratio hypothesis

(Barbour *et al*. 1999)

- Species occurrence during succession is ultimately a function of:
  - What gets there 1<sup>st</sup> & establishes (dispersal and colonization → regional filters)
  - What can survive & reproduce (biotic interactions → local filters)
- Typically, colonization sequence matters



- What is a "natural" disturbance?
  - Relatively discreet event in time that disrupts ecosystem, community and/or population structure, and changes substrate and resource availability, and the physical environment
    - Natural in the sense that the resident organisms evolved in the presence of that disturbance → capacity to resist &/or recover
    - Complex & synergistic  $\rightarrow$  E.g., drought + disease + fire
    - Disturbances are characterized by type, severity, intensity, frequency, size, timing, etc. (= disturbance regime)
    - For most ecological systems, disturbance regime is a mix of large infrequent and small frequent events

- Disturbance "resets" the successional clock
  - Natural disturbances are not "bad"
    - Play a large role in shaping ecological communities
    - Fire, wind, DIPs, floods, landslides, volcanos, earthquakes, etc.
    - Eliminated from, introduced to, and/or drastically changed in many ecological systems
      - Restoration often involves restoring natural disturbance regimes
         &/or eliminating those that are not natural (e.g., fire, floods, etc.)
  - Anthropogenic disturbances are typically "bad"
    - Most often detrimental  $\rightarrow$  little evolutionary adaptation
      - Restoration typically involves 1<sup>st</sup> removing the disturbance (e.g., fire, nonnative herbivores, etc.)

- Type of fire
  Surface, crown, ground
- Mean Fire Return Interval
- Severity/Intensity





#### **Crown Fire**



High Intensity, High Severity Postfire succession: Dominated by species adapted to colonize following fire

#### Surface Fire



Low Intensity, Low Severity Postfire succession: Dominated by species adapted to survive fire

• Succession – Gap Phase Dynamics (frequent, small events that allow shade intolerant species to persist)





• Anthropogenic disturbances (typically far outside of the HRV for a given ecological system)





• Nonnative, invasive species



**Feral Pigs** 



#### Quadrastichus erythrinae



Psidium cattleianum



#### Pennisetum setaceum



• Fixed endpoint (steady state) vs. multiple possible endpoints (alternative steady states)



 Alternative stable states (i.e., multiple possible endpoints) have very large implications for restoration (choice of species, establishing targets, monitoring success, etc.)



(Bullock et al. 2011)



(Mayer & Khalyani 2011)

- Ecological systems are dynamic and ever-changing
  - Deterministic and stochastic disturbance events are the norm
  - Increasingly shaped by human activities
    - In reality humans have shaped ecological systems ever since they evolved and always will
  - No simple or universal answers to guide restoration
    - Often system dependent
    - General conceptual frameworks are still being debated
      - Ecological theory can reduce risk of unpredicted/undesired restoration outcomes
      - Ecological restoration can inform ecological theory

- Contrasting general patterns of successional (or restoration) trajectories
  - -Same starting point, different end result



(Suding & Gross 2006)

- Fast vs. slow processes (mechanisms of change)
  - Dynamics occur on different scales of space, time, and ecological organization (continuum of time, space, & organizational level)
  - Fast: occur at individual or population levels, &/or small spatial scales
  - Slow: occur at ecosystem or landscape levels, &/or large spatial scales

	Speed/Scale	Level	Attributes of Change	
			Structure	Process
	Fast/Small	Individual	Physiology Behavior Size	Mortality Growth Reproduction
		Population	Density Structure (age, size, genetic)	Evolution Extinction
		Community	Diversity Composition Functional groups	Coexistence Competition Mutualism Predation
		Ecosystem	Nutrient Pools/Production	Resistance Resilience Nutrient flux/retention
(Suding & Gross 2006)	Ļ	Landscape	Exogenous Disturbance Propagule pressure	Connectedness Colonization
	Slow/Large	Region	Temperature Precipitation	Pollution inputs Climate change

• Equilibrium vs. Multiple Equilibrium vs. Non-equilibrium

TADIEO1

General theories that attempt to predict how the composition and function of systems change over time and/or behave following a disturbance.					
Assumptions	Climax equilibrium, uni- directional, continuous	Equilibrium, multidirec- tional, discontinuous	Persistent non-equilib- rium, nondirectional, discontinuous		
Permanent states	One (climax)	More than one	None		
Trajectories	Convergent	Regime shifts, collapses	Divergent, arrested, cyclic		
Predictability	High; based on species at- tributes	Moderate; possible but difficult	Low; chance and legacies important		
Important factors	Species interactions, ecosystem development	Initial conditions, positive feedbacks, landscape position	Chance dispersal, stochas- tic events		

- Single Equilibrium Endpoint
  - Return to a pre-disturbance state following disturbance
    - Steady directional change to a single endpoint
    - Predictable consequence of species interactions
    - Strong internal regulation via negative feedback mechanisms
  - Restoration can accelerate succession by skipping some points along the continuum
    - e.g., Restoring fire and flood regimes
    - Likelihood depends upon level of degradation and isolation



• Multiple Equilibrium States

(Suding & Gross 2006)

- Often occurs with little forewarning  $\rightarrow$  identifying thresholds?
- Change is discontinuous, abrupt and has multiple trajectories
  - e.g., overgrazing and woody invasion in grasslands
- Restoration must identify the positive feedbacks that maintain a degraded state, and eliminate them
  - e.g., invasive species/wildfire cycle in Hawaii
- Restoration can result in unintended trajectories
  - e.g., removal of fountain grass in degraded dry forests in Hawaii



- Persistent Non-equilibrium State
  - Assumes external factors (e.g., chance events & biological legacy) are more important than internal factors (e.g., biotic interactions)
  - Unpredictability of succession
  - Divergent, cyclic or arrested trajectories
  - Chance colonization, stochastic disturbance events
  - Restoration perspective
    - Most likely to occur in fragmented areas, w/ loss of propagule source, and in highly variable and degraded abiotic environment
    - Focus on restoring function instead of species assemblages



B) Persistent non-equilibrium

(Suding & Gross 2006)

- Potential ways in which community ecology theory can inform/advance restoration science and practice
  - What types of trajectories characterize the recovery of degraded ecological systems?
  - Can we predict the endpoints of succession? Of restoration trajectories?
  - How do dynamics that occur on very different scales of space and time relate to one another?
  - How much variability does an ecological system require for adequate recovery and adaptive capacity for change in the future?

1. Ecological systems are dynamic and ever-changing, both spatially and temporally.

2. Disturbances are natural components of all ecological systems, and the resident organisms are typically well-adapted to that system's natural disturbance regime (i.e., type, frequency, intensity, etc.). For most ecological systems, the natural disturbance regime is a mix of large infrequent events, and small frequent events (not necessarily of the same disturbance type).

3. Disturbances initiate ecological succession, which is a directional change in species composition, structure, and resource availability over time that is driven by biotic activity and interactions, and changes in the physical environment. Ecological succession is often differentiated into primary (no soil or plant propagules on site) vs. secondary (at least some soil and plant propagules on site). Restoration typically occurs via secondary succession, although primary succession is likely to more applicable in very degraded sites (e.g., mine reclamation).

4. Many ecological systems are characterized by alternative/multiple stable states, which has very large implications for restoration (e.g., choice of candidate species, establishing targets, monitoring success, etc.). In these systems, alternative states are triggered by thresholds that, once crossed, maintain the system in an alternative state via positive feedback mechanisms. Restoration to a different state requires disruption of these positive feedback mechanisms.

5. Highly degraded systems are often characterized by a persistent non-equilibrium state where external factors (e.g., stochastic events and biological legacies) override internal factors (e.g., biotic interactions). In such cases, restoration is much more likely to succeed if the focus is on restoring function over species assemblages.