- Objectives:
 - Ecology and management of invasive species in a restoration context
 - In most cases, impossible to talk about restoration ecology without explicitly considering invasive species
 - What is an invasive species? What determines invasion success?
 - Invasive species as drivers vs. passengers of ecological change
 - Active vs. preventative management of invasive species
 - Is there a place for nonnative species in ecological restoration?
 - Novel Ecosystems

• Ecological Hierarchy



- What is an invasive species?
 - Invasive species (USDA NISIS):
 - (1) nonnative to the ecosystem under consideration, and
 - (2) whose presence causes or is likely to cause economic or environmental harm, or harm to human health
 - Invasive species (Richardson et al., 2011):
 - Alien species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in very large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances, possibly leading to adverse effects on invaded habitat.
 - Alien, invasive, nonnative, exotic, naturalized, weed, casual, transformer, etc.

- How do invasive species cause "harm"
 - Economic
 - >\$120 billion annually in the U.S. (Pimentel et al. 2005)
 - \$1,100 per household
 - \$3 million per year per infested power plant for zebra mussel
 - \$3 million per year in Florida for Melaleuca invasions
 - Health
 - Introduced pathogens and diseases (e.g., West Nile virus; Am. chestnut blight; Dutch elm disease; ohia rust; etc.)
 - Introductions result primarily from travel and international commerce

- How do invasive species cause "harm"
 - Biodiversity
 - Invasive species are 2nd most important cause of loss of biodiversity
 - In the U.S., >1/2 of the species listed as threatened or endangered are at risk due to competition with or predation by nonnative species
 - Ecological systems; Ecosystem processes/functions; Ecosystem goods and services
 - Invasive species alter:
 - Disturbance regimes
 - Nutrient cycling
 - Hydrology
 - Carbon cycling
 - Etc.

• Terminology, terminology, and more terminology

Table I Recommended terminology in plant invasion ecology

Alien plants1	Plant taxa in a given area whose presence there is due to intentional or accidental introduction as a result of human activity (synonyms:
Casual alien plants	exotic plants, non-native plants; nonindigenous plants). <i>Alien</i> plants that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence (includes taxa labelled in the literature as 'waifs', 'transients', 'occasional escapes' and
Naturalized plants	'persisting after cultivation', and corresponds to De Candolle's (1855, p. 643) usage of the term 'adventive' ²). <i>Alten plants</i> that reproduce consistently (cf. <i>casual alten plants</i>) and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants, and do not necessarily invade
Invasive plants ²	natural, seminatural or human-made ecosystems. Naturalized plants that produce reproductive offspring, often in very large numbers, at considerable distances from parent plants (approximate scales: > 100 m; < 50 years for taxa spreading by seeds and other propagules ⁴ ; > 6 m/3 years for taxa spreading by roots,
Weeds	rhizomes, stolons, or creeping stems), and thus have the potential to spread over a considerable area. Plants (not necessarily <i>alien</i>) that grow in sites where they are not wanted and which usually have detectable economic or environmental effects (synonyms: plant pests, harmful species; problem plants). 'Environmental weeds' are <i>alien plant</i> taxa that invade natural vegetation,
Transformers ⁵	usually adversely affecting native biodiversity and/or ecosystem functioning (Humphries <i>et al.</i> , 1991; Randall, 1997). A subset of <i>invasive plants</i> which change the character, condition, form or nature of ecosystems over a substantial area relative to the extent of that ecosystem.

(Richardson et al. 2000)

- Terminology, terminology, and more terminology
 - Invasive species need to, by definition, overcome multiple barriers (Richardson et al. 2000):
 - 1) *Introduction*: arrive at a site outside of their previous geographical range
 - 2) *Colonization*: reproduce and increase in number to form a colony that is self-perpetuating
 - 3) Naturalization: establish new self-perpetuating populations, undergo widespread dispersal, and become incorporated within the resident flora
 - Lots of species get past #1, but a very small fraction can overcome #s 2 and/or 3

- What determines invasive species success?
 - Very few introductions lead to invasions
 - Nonnatives have not evolved in the new system
 - Lack pollinators, seed dispersers, mutualists, etc.
 - Invaders not resistant/resilient to natural disturbance regimes, herbivores and predators, etc.

- Those that are successful are often drastically so

- Superior competitors
- Evidence for rapid, genetic adaptation on short time scales
 - EICA (Evolution of increased competitive ability)
 - » Evolution of greater size/fecundity in introduced environment
- Enemy release hypothesis
- Novel weapons hypothesis
 - Allelopathy
- All of these purported mechanisms have support in the literature

Pre-human Hawaii



Produced by the Hawai'i Natural Heritage Program, June 2003

•Present day Hawaii



- Why worry about invasive species?
 - Present in almost all ecological systems
 - Island ecosystems particularly vulnerable to invasion
 - Lots of past focus on impacts on biodiversity, more focus now on impacts on ecosystem processes
 - Still have relatively poor understanding of ecological impacts of invasion in most cases
 - Elimination of invaders and restoration of pristine species assemblages likely impossible in many cases
 - Need better understanding of ecological impacts of invasions
 - Need better understanding of how to deal with invasions in a restoration context

• Are invasive species the drivers or passengers of ecological change in degraded ecosystems?



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(Didham et al. 2005)

- Are invasive species the drivers or passengers of ecological change in degraded ecosystems?
 - Invasion cannot be explained solely by competitive ability (MacDougall & Turkington 2005)

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• Need a broader context of environmental change, evolutionary adjustment, and life history tradeoffs



- Management and preventive approaches
 - Depends on the state of degradation & causal agents
 - Prevention management \rightarrow relatively pristine state
 - Active management (i.e., removal) \rightarrow degraded state



(D'Antonio & Chambers 2006)

- Management and preventive approaches
 - Prevention management
 - Ecosystems currently providing valuable services and intact structure/processes
 - Maintain or increase stability (resistance and resilience)
 - Manipulation or maintenance of properties that favor persistence and recovery of native species assemblages
 - Necessitates knowledge of controls over resistance and resilience

- Management and preventative approaches
 - Active management (i.e., restoration)
 - Following establishment of invaders and changes in ecosystem properties and processes
 - Top-down control: removal/elimination of invader
 - Manual removal, herbicides, biological control
 - Control of propagule pressure from surrounding area
 - *Bottom-up control*: restoration of properties or processes that contribute to stability (and sustainability)
 - Manipulation of disturbance regimes
 - Manipulation of soil conditions to favor desirable species
 - Direct seeding of desired species

- Management and preventative approaches
 - E = f(I,S)
 - E = # of successful invaders, I = # of species introductions, and S = survival and reproduction of introduced species
 - Managing I is the most cost-effective and easiest; requires information on:
 - Presence in region, or likelihood of arrival
 - Dispersal and life-history traits
 - Managing S requires information on:
 - Dispersal and life history traits (e.g., r-k theory)
 - Population, community, ecosystem, and landscape ecology

- Management and preventative approaches
 - Successional theory can inform invasive species management
 - Potential influence of invaders on species composition:
 - Facilitation ("invasional meltdown" vs. "benevolent invaders")
 - Inhibition (long term vs. short term)
 - No impact (then is it really an invasive species?)
 - Taking advantage of "lag phases"
 - Targeting outlying (satellite) populations
 - Manipulation of disturbances
 - Reinstating disturbance
 - Removing disturbance
 - Type, timing, intensity, etc.

- Management and preventative approaches
 - Competition theory
 - At local scales, competition structures plant assemblages
 - Abundant natives \rightarrow resource availability scarce for invaders
 - Many invaders are superior competitors though
 - » Most need disturbance to become established (i.e., passengers of change)
 - Utilization of unexploited niches
 - High biodiversity does/does not lead to invasion?
 - Resource supply is key
 - Also depends on spatial scale



(Stohlgren et al. 2008) ¹⁹

- Management and preventive approaches
 - Fluctuating resources hypothesis
 - Invasibility is a function of resource availability (= gross resource supply rates - resource uptake)
 - Resource availability increases with:
 - » Disturbance
 - » Climate Change
 - » N deposition
 - Removal \rightarrow further invasion?
 - Manipulating resource supply
 - C amendments to soil



(D'Antonio & Chambers 2006)

- Are nonnative species always "bad" in restoration?
 - Not all nonnatives are necessarily "bad" (Ewel & Putz 2004; A place for alien species in ecosystem restoration)
 - Many "fade out" naturally over time
 - Management would be a poor expenditure of resources
 - Can be used to facilitate desirable species
 - "Benevolent" invaders
 - Many nonnative species "outperform" natives
 - High provisioning of ecosystem goods and services
 - Particularly in highly degraded systems where "desirable" native species are not likely to establish or be competitive
 - Should nonnative species ever be used intentionally in restoration? Why/why not?

- Are nonnative species always "bad" in restoration?
 - Not all nonnatives are necessarily "bad" (Ewel & Putz 2004; A place for alien species in ecosystem restoration)





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- Novel Ecosystems
 - "Novel", "emerging", or "no-analog" ecosystems
 - Ecosystems that differ in composition (&/or function) from present & past ecosystems
 - Species that occur in combinations &/or relative abundances that have not occurred previously within a given biome
 - Arise via human action, abiotic drivers (e.g., climate change), and/or biotic drivers (e.g., introduction of nonnative species)
 - Likely to be cost prohibitive (or simply impossible) to return these systems to some pre-disturbance reference state
 - What value do novel ecosystems have?
 - » How can they be utilized in a restoration context?
 - » Do they have characteristic structure and function?
 - » What ecosystem goods & services do they provide?

- Novel Ecosystems in a Restoration Context
 - In Hawaii, novel forests store and sequester C at rates equivalent to or in excess of native forests



(Mascaro et al. 2012)

- Novel Ecosystems in a Restoration Context
 - Historic vs. Hybrid vs. Novel (Hobbs et al. 2009)
 - Hybrid retains characteristics of the historic system but composition &/or function now lies outside the HRV
 - Novel is one in which the species composition and/or function have been completely transformed from the historic system
 - Should novel ecosystems be restored? Can they be restored?

- Novel Ecosystems in a Restoration Context
 - Ecosystem trajectory depends largely on whether abiotic & biotic alterations occur separately or in concert



- Novel Ecosystems in a Restoration Context
 - "Retaining the somewhat static view of ecosystems as particular assemblages in particular places will become increasingly unrealistic and is likely to shackle conservation and restoration efforts to ever more unrealistic expectations and objectives. A more dynamic and flexible approach might not involve throwing out all previously held values and norms entirely, but could require serious consideration of a range of approaches to deal with an increasingly uncertain future."

 Invasive species are those that are not native to a region, reproduce and sustain self-replacing populations, spread outside of the introduced range, and result in changes to ecosystem structure and/or function. There are many terms that are used, often erroneously, to refer to invasive species including alien, naturalized, weed, non-native, etc.

2. Very few introductions of non-native species ultimately become invasive species, but those that do often do so drastically. To become invasive, a species must overcome the barriers of introduction, colonization, and naturalization. From a cost-benefit standpoint, management of invasive species should concentrate on reducing/eliminating introductions in the first place.

3. Management of invasive species can be categorized as preventive vs. active management. Preventive management entails managing an ecosystem to be resistant to invasion before it becomes degraded and invaded. Active management, on the other hand, includes top-down and bottom-up activities to eliminate or control existing invasions in areas that are already degraded (i.e., manipulation resiliency).

4. Knowledge of ecological theory (e.g., successional dynamics, biotic interactions, resource availability and use, etc.) can and should be used to inform management actions taken to prevent and/or control invasions. This includes considering if the presence of an invasive species is always "bad" and, therefore, if active management is even needed, when it is needed, etc.

5. Novel ecosystems (i.e., those that differ in composition &/or function from present & past ecosystems) are an increasingly common phenomenon across the globe. Given the rapid pace of global change (e.g., climate change, N deposition, invasive species, etc.), should (or even can) these systems be restored to some historical reference state?