Salt Marsh Secrets

Who uncovered them and how?

By Joy B. Zedler

An e-book about southern California coastal wetlands for readers who want to learn while exploring

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This e-book records favorite stories about salt marsh secrets that my collaborators and I uncovered while studying southern California coastal wetlands, from the 1970s to date. In 1986, we became the Pacific Estuarine Research Lab.

Please download the files as they appear online and enjoy learning what we learned…and more. You'll meet many "detectives," and you'll be able to appreciate how they learned so much--undeterred by mud and flood. Learn while exploring the salt marshes near you!

Each chapter (1-21) is being posted at the TRNERR as a separate file (PDF).
Chapter numbers precede page numbers (for chapter 1: 1.1...1.14).
Layout by Emily L. Rosenthal. Photos by the author or as noted.

PDF name and brief description:

Transitions:
From marsh plain to high marsh & from salt marsh to upland

In chapter one, I described how vegetation changes with elevation. It's not a smooth gradient from low to high; however. There are two transitions where tidal influence changes rapidly: from the broad marsh plain to the high marsh and from the high marsh to the upland. Transitions are places where changes in species distributions occur rapidly, relative to the variations on either side. Another word used to describe changes between vegetation types is ecotone.

At least three definitions of "ecotone" appear in the ecological literature:

1. A steep gradient between more homogeneous patches of vegetation.
2. A transition between patches.
3. Zones of turnover in species between two relatively homogeneous areas.

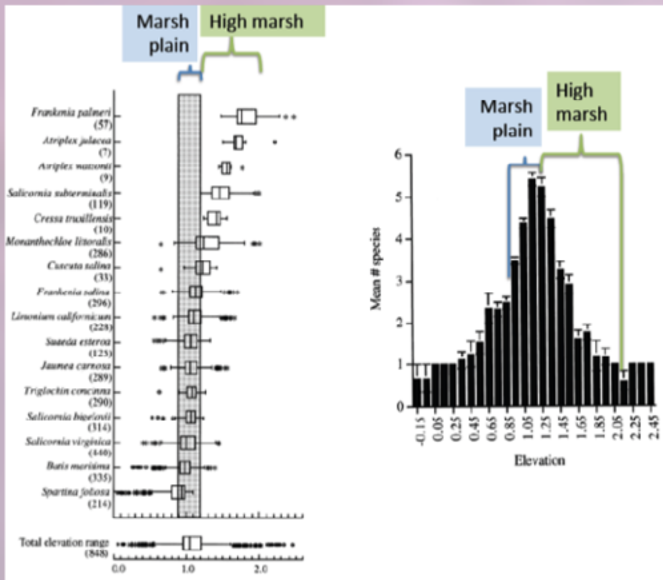
Here's my definition: An ecotone is a narrow strip, usually vegetated, that occurs between larger areas of different vegetation. Sometimes the vegetation that forms a narrow band in one area, such as along a steep slope, can form a broad patch elsewhere, where the slope is gentle. As a result, a narrow ecotone in one landscape might be broader elsewhere. At a very large scale, some consider the entire salt marsh to be an ecotone between bays and uplands. It's the smaller scale patterns that intrigue me. Here, let's uncover some secrets about transitions from one salt marsh community to another.

Are ecotones more diverse than adjacent vegetation?

Ecotones are thought have more species than adjoining areas and thus higher conservation value. But there are at least two more hypotheses about cause → effect. Higher species richness could simply result from the overlap of species from the two adjacent patches. Supposing one large patch has 9 species and the other has 6; the ecotone could support all 15. Alternatively, an ecotone could support species that are specialized to occur at the edges of the two adjacent plant communities. It could add one or two species, bringing the ecotone diversity to 17 (2 + those from neighboring vegetation). Our southern California salt marshes have ecotones between the marsh plain and the high marsh, as well as between the high marsh and the upland. Take a guess—will the ecotones be more species rich than vegetation below or above each transition?

THE TRANSITION FROM MARSH PLAIN TO HIGH MARSH. We can look to the salt marshes of San Quintín Bay for clues about the species richness of ecotones versus downslope and upslope vegetation. The upland and the wetland-upland ecotone are much drier and desert-like, however, and there are different dominant plants. So, we should not extrapolate patterns in the wetland-upland ecotone at Volcano Marsh to describe historical ecotones in southern California. We can, however, use the data to examine marsh plain-high marsh ecotones, because species composition is very similar to that in southern California, based on over 800 0.25-m^2 plots that we sampled. Was species richness higher at the ecotone between the marsh plain and high marsh at Volcano Marsh than in either of the adjacent plant communities?

Here are graphs from chapter one, to help uncover secrets about a salt marsh ecotone:



First, how many marsh-plain and high-marsh species cross the ecotone? Which are high marsh species that occur on the marsh plain? Which marsh plain species extend into the high marsh?

To answer these questions, we have to impose a discrete boundary (perhaps the 1.2-m elevation) onto a pattern of change that is more gradual. Then, we have to assign species to one or the other communities. One high marsh species and 2 marsh-plain species are relatively common at the 1.2-m elevation. One species' distribution is centered on the 1.2-m line—the parasitic dodder (*Cuscuta salina*). So the ecotone count = 4.

Let's check the total species that occurred primarily in the high marsh (6?) and in the marsh plain (8?). Overall, at the whole-marsh scale, the ecotone, with 4 species, is less diverse. Still, there is one "ecotone species."

> Dodder has no chlorophyll and cannot photosynthesize; hence, its seeds have to land on a suitable host and receive enough moisture to germinate and immediately penetrate the host's leaf or stem tissues. Dispersal of floating seeds at a specific "tidal season" (see chapter two) would foster its occurrence within a narrow elevation range. So would the stress of prolonged inundation below the ecotone and prolonged exposure above the ecotone.

We can also ask how many species occur per plot at the elevation range centered at 1.25 m compared to neighboring elevation classes. In the bar graph, plots at the ecotone average over 5 species, while those downslope have 3-4, and those upslope average around 1-4. So at the plot scale, the ecotone, with 5 species, is more diverse. The plot-scale data support the hypothesized species-rich ecotone and both hypothesized causes (overlapping species and an ecotone species, dodder). We can argue the outcome either way.

> There's a lesson here. In setting up hypotheses, one should clearly identify how it will be tested (marsh scale or plot scale) and the criterion for deciding the outcome (the simple sum of species or a statistically significant difference?). One can also set up alternative hypotheses, one for each scale.

THE TRANSITION FROM SALT MARSH TO UPLAND. I would like to know more about the historical ecotone between southern California salt marshes and their upland coastal scrub vegetation. Unfortunately, centuries of human disturbance have altered historical patterns. Too much of the salt marsh-upland ecotone in our region has been farmed, covered with urban developments, or disturbed by trails and off-road vehicles and dumping grounds. As a result, too little area remains, and the tiny remnants have many exotic invasive plants and probably only a small sample of their historical native species, both plant and animal. Here's an example at Tijuana Estuary, just west of the Visitor Center.

The high marsh-upland transition is also where exotic plants invade. Increased freshwater inflows reduce soil salinity in the high marsh transition. Seeds of the following can then germinate. Here are common invaders:

Rabbitsfoot grass	*Polypogon monspeliensis*
Sickle grass	*Parapholis incurva*
Rushes	*Scirpus* spp.
Ice plant	*Carpobrotus edulis*
Brass buttons	*Cotula coronopifolia*
Cattail	*Typha domingensis*
Curly dock	*Rumex crispus*
Fivehorn smotherweed	*Bassia hyssopifolia*
Prickly Russian thistle	*Salsola tragus*
Australian salt bush	*Atriplex semibaccata*
Myoporum or Ngaio tree	*Myoporum laetum*

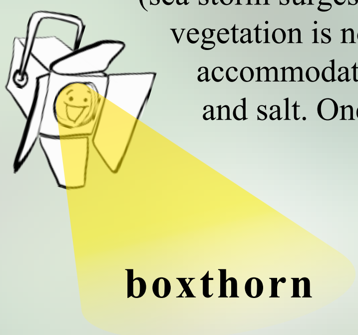
The ecotone from salt marsh to upland at Tijuana Estuary has a long history of disturbance, but many native plants are still present. What restricts the ecotone species from venturing further upslope into the coastal scrub? As in the salt marsh, the answer seems to be salt and water. Here is my thought about the upper limit of high marsh plants. I think glasswort and love grass are restricted by summer drought. Even though tidal inundation is rare, the deep roots of perennial plants should be able to tap into groundwater. Some groundwater monitoring and studies of roots are needed!

Studies of terrestrial plant roots involve inserting clear plastic pipes into the soil for roots to grow around and become visible using a "root periscope" with tiny light and microscopic camera. That's an adaptation of medical technology for looking into lungs or other body cavities. The technology exists; someone needs to use it to reveal halophyte root secrets. You could be that someone!

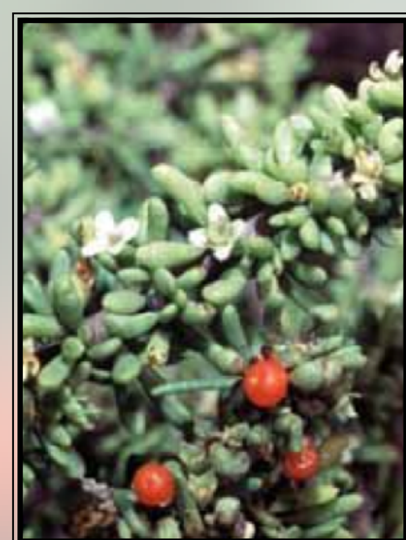
I speculate that the ecotone doesn't move further downslope because terrestrial (upland) plants don't tolerate the occasional seawater inundation. Even brief anoxia is a stress for terrestrial plant roots.

I don't think salt limits high marsh species from extending upslope into the upland ecotone, because salt spray extends even further inland than storm-driven waves. I do think the ability of high marsh species to move inland is limited by dry soil and competition with coastal sage species. As sea level rises (actually, it's already rising, but it is projected to rise more rapidly around the year 2050), it will be possible to witness the migration of at least some salt marsh species. Which salt marsh halopytes will move inland? In chapter nineteen, I develop several hypotheses about the species that will persist longest on the marsh plain and which will migrate upslope. Others will probably need our help to remain in the region.

As salt marsh species are moving inland, which coastal scrub species will retreat as sea level rises? I think the marshward edge is too salty for coastal sage species. During overwashes (sea storm surges) and with rising sea levels, it might also be too wet. Coastal sage scrub vegetation is not likely to have lots of aerenchyma in plant roots or adaptations for accommodating salt. Still, some upland plants can tolerate drought and brief inundation and salt. One native shrub deserves the spotlight….



Boxthorn (*Lycium californicum*) is an unusual, spiny shrub that is salt-tolerant like salt marsh plants and dormant in winter like the coastal scrub! Its 3-5-mm leaves appear in the cool moist season. Its red fruits are small (2-3 mm) but juicy. Does it surprise you that this shrub is a member of the tomato family?



Matt James uncovered many of the secrets of boxthorn. This woody plant grows well in the high marsh-upland ecotone--a very narrow habitat between the highest high tides and the nontidal upland. Recently, boxthorn was recognized as a sensitive species, thanks in part to Matt's research on this species' rarity and functions (James and Zedler 2000). Boxthorn is now included in the California Native Plant Society's Inventory of Rare and Endangered Plants.

Here are some of its important functions: Boxthorn feeds pollinators when it is flowering and its red berries attract frugivores (fruit eaters), including birds and small mammals. The plant's vertical structure offers perches for birds and branches for lizards to climb. Matt found runways under the shrubs, which were evidence of animal use, perhaps as a refuge from predators. Boxthorn also provides "crutches" for other plants, such as salt grass, to grow up through its canopy.

You know you're near the upper limits of a saline wetland when you walk downslope and see boxthorn. When you spot a tall boxthorn, see if other plants are using it as a crutch.

Here's boxthorn during its cool-season active period (Nov. photo) and during its summer dormant period (June photo).

The marsh-upland transition combines subshrubs from the high marsh and the coastal sage scrub.

> A subshrub is a short, woody perennial plant. Shrubs of the coastal sage scrub and chaparral are taller, more sturdy woody plants, but still not trees, which are even taller. Glasswort is another subshrub of the high salt marsh.

Subshrubs in Sweetwater Marsh, along San Diego Bay

Both glasswort and alkali heath grow taller and denser canopies in the transition than they do in the salt marsh. Joining the mix from the upland side, you might find flat-topped buckwheat (*Eriogonum fasciculatum*), goldenbush (*Isocoma menziesii*), saltbush (*Atriplex lentiformis*), wooly sea blite (*Suaeda taxifolia, S. calceoliformes),* bladderpod spiderflower (*Isomeris arborea*), and perhaps white sage (*Salvia apiana*) and black sage (*S. mellifera*). There are many transition species, and there is much to learn about how they function.

How can a woody perennial plant establish seedlings in the transition between the regularly-inundated salt marsh and the nontidal upland. When would the seeds germinate? When would the roots of seedlings be deep enough to obtain moisture from dry soil between rainfalls? What would the shrub have to tolerate in order to persist through dry summers?

Transition species have to withstand storm surges (occasional seawater above the high tide line) as well as drought, and high salinities from surges and salt spray. Life near the coast is rather stressful for tall woody plants, because fine layers of salt are often deposited on leaves by mild breezes. Heavy salt spray during persistent winds can actually "prune" tall long-lived plants, making them lopsided, with branches that are more diminished on the windward side than in the lee of the wind.

Salt collects on the leaf surface, where it can draw water from the plant if there's no thick waxy coating (called a cuticle). Salt has a similar effect when it falls on the soil and makes its way towards roots. Unlike a mobile animal, a perennial plant is stuck in one place. Plants can't escape stress so it has to minimize salt stress. What adaptations might accomplish this? Here are five:

(www.smmflowers.org/bloom/pics/)

- Be deciduous—drop all leaves in the hot dry summer when there is little water in the soil. We learned that the leaves drop due to drought, rather than depending on a cue from summer day length. When a pipe along the McCoy Trail leaked salt water at the base of a boxthorn plant, boxthorn grew robust and remained green all year!
- Have succulent (juicy) leaves that can hold onto water from the previous rainfall. Succulence, however, might attract herbivores, such as rabbits, both for the calories and the water.
- Because succulent leaves are attractive to herbivores, grow thorns to discourage grazers (animals that eat grasses and forbs) and browsers (animals that eat twigs and other tough foods).
- Produce colorful berries for birds to eat and seeds that don't get digested in the bird's gut. Then the seeds will be widely dispersed. Stiff twigs offer a perch for a bird to sit and feed. As birds move from one shrub to another, they could perch for awhile, digest the fruit from other shrubs and dump their load of indigestible seeds. Look for bird droppings under shrubs that have tall, stiff twigs and edible fruits.
- Spread vegetatively as a clone.

Boxthorn has all these adaptations. It tolerates the usually-saline, often-dry transition from salt marsh to upland. Its fruits and succulent leaves provide very good reasons for animals to visit (FOOD and habitat). Being green and flowering in winter complements (enhances without duplicating) the functions of the salt marsh, which is semi-dormant in winter.

Is this a superplant, capable of diverse functions that serve wildlife year-round? I think so, but it would be great to have more data on animal use. Does it deserve special conservation status? I know so.

Despite being well-adapted to the transition, boxthorn's population has declined. Why? First, the transition is a narrow elevation, usually along steep slopes or banks, where there was never much space. Second, humans have severely encroached on the habitat that did exist historically—not just by trampling and paving, but also by filling with spoils, often deliberately, to raise the ground level.

Matt James learned that boxthorn was restricted to a 1.1-meter elevation range near the Visitor Center at Tijuana Estuary. Glasswort (a salt marsh subshrub) occurred downslope and flat-top buckwheat (a coastal sage scrub subshrub) occurred upslope. To figure out what restricts boxthorn's distribution, Matt set up a clever greenhouse experiment to test how each member of the trio (3 species) are affected by soil moisture and salt. He asked: What allowed the seed germination and seedling establishment during wet winters? Can older plants persist as the seasons change from moist winter to dry summer? And, because boxthorn was more easily propagated from cuttings than from seed, he also asked how salt tolerant are the branch cuttings from mature plants in the field?

As predicted, the wetland halophyte, glasswort, tolerated more salt and needed more water to germinate and establish seedlings, explaining this species' restriction to the tidal marsh. At the opposite extreme, buckwheat seeds could not germinate in soil wetted by seawater. Salt water (and anoxic soil?) also killed seedlings and older plants, likely confining buckwheat to areas further upslope.

The response of boxthorn was very informative and exciting! Regular wetting by seawater killed seedlings, while cuttings tolerated some seawater exposure. Thus, we concluded that both boxthorn and buckwheat could establish seedlings following salinity-reduction during heavy wet-season rainfall, but subsequent droughts and saline conditions would eliminate buckwheat. Only boxthorn would persist.

This conclusion was further supported by a second innovative experiment with seedlings of all three species and declining water tables: Matt placed seedlings in clear plastic tubes and varied rates of freshwater recession. Boxthorn and buckwheat seedlings were more tolerant of dry conditions than glasswort seedlings.

(www.fws.gov/nwrs/twocolumn.aspx?id=48632)

In 2000, we advised that the transition between the salt marsh and coastal sage scrub should be protected and restored to support this rare ecotone species. Designating boxthorn as a sensitive species was a positive first step. This species is rare, mostly because its habitat is either gone (urbanized) or degraded (overused for paths and invaded by weeds).

• Here's a simple calculation: You can show that transition habitats are narrow where slopes are steep. Compare the area of an intermediate elevation where the topography slopes gradually vs. steeply. You can do this at home by calculating the hypotenuse for x = 10 vs. x = 100 and y = a constant = 5 meters. The length of the hypotenuse is much greater for a gentle than a steep slope. A plane along a gentle slope would be larger than for a steep slope.

• If you'd like to learn more about narrow transitions between two broader habitats, try searching for information using the term, ecotone. Be aware, however, that one person's ecotone is another person's broader habitat.

• Be aware that ecotones are dynamic and can change over time, not just over landscapes. A narrow band can expand over a series of wet years; a broad band can shrink during "hard times."

In her PhD research at UC-Davis, Bibit Traut considered the high marsh to be the ecotone between the marsh plain and the upland. As discussed above, the term is relative. It depends on what is narrow in between two wider habitats.

In northern CA salt marshes, she explored the high salt marsh's role in trapping nitrogen from the upland and the role of the subshrub canopy in supporting spiders. Her three main conclusions (Traut 2005) were:

The high salt marsh supported unique vegetation and accumulated more soil nitrogen than the upland.

The richness of both plant and spider species increased with elevation, leveling off in the upland.

The ecotone had complex vegetation that supported more spider species than the upland.

Here's a funnel-shaped spider web in the high marsh at Tijuana Estuary (photographed in June 2014). The canopy structure that supports the web includes glasswort, alkali heath, and love grass.

Visit the high marsh on a dewy morning or evening when drops of moisture turn spiderwebs into sparkling "marsh jewelry."

Read Bibit Traut's (2005) work and conduct similar studies in southern California. We need to know more about the spiders and other arthropods that live next to our salt marshes.

More about ecotones...in southern Chile

(www.giantbomb.com)

Some ecologists regard ecotones as dynamic components of landscapes. Perhaps they support higher productivity, especially if they support additional species.

In January 2014, my Botany colleague, Dr. Linda Graham, and I led a class of 10 UW undergraduates to Torres del Paine National Park, within Patagonia, Chile. Our native guides were Dra. Patricia Arancibia (U. Bio Bio) and Nicolas Galleguillos (Santiago, also a UW MS student). In the Patagonian steppe, the students examined the numbers of plant species (species richness) within narrow wetland-upland ecotones.

We asked a basic question: How many plant species do ecotones support, compared to communities on either side? The students had read conflicting results in the published literature, so we hypothesized that ecotones could be species-rich, species-poor, or similar to neighboring vegetation.

The Patagonian landscape is fascinating, with dry grasslands (steppes) pitted with shallow temporary wetlands (vegas), and guanacos grazing across boundaries. The vegas are the guanaco watering holes, and the grasslands provide forage and bare-dirt depressions used for dust baths. I was privileged to see them roll in the dust-tub and then shake off the dirt in the incessant (never-ending) wind. That behavior showed how a perfect oval-shaped dust-tub forms!


Photo: National Wildlife Federation


Photo: Martin Feehan

We stretched transect lines from each vega across the ecotone and into the steppe. Then we recorded the numbers of plant species in contiguous plots (touching one another along a transect line), each 0.25-m^2. The vegas were green and moist; the ecotones were obvious 2- to 3-m-wide transitions, and the steppe was dry with dominant grasses. We easily classified each plot into one of the three habitat types, based on the dominant species and environmental conditions.

During our short visit to Patagonia, we didn't have enough time to sample as many vega-ecotone-steppe transects as I would have liked. So our results are very preliminary. We found that the vegas averaged 9.0 plant species per 0.25 m^2; the steppes had 5.9, and ecotone had 10.0. The vega-type wetland seems to add considerable biodiversity to the landscape, but there also seems to be an "ecotone species." One grass occurred in the ecotone but not in vega or steppe plots. We recommend further research (and we hope Chileans will follow up!).

More about ecotones...in Quebec

Closer to home (well, Canada is closer than Chile), I found a study that shows how wetlands add diversity to a forest landscape. In Quebec, several kinds of wetlands (lakeshores, ponds, swamps, glades, and streamsides) cover only 1.1% of an old-growth forest reserve but support 45% of the reserve's plant species!

The wetlands contribute 280 species of vascular plants, almost as many as in the remaining 98.9% of the reserve. That's what we call a disproportionate contribution. Most of the species occur in the least extensive landscape component (wetland)! Local diversity was also much higher for the wetlands than for the surrounding upland forests. The results of this study (Flynn et al. 2008) strengthen the need to conserve wetlands among uplands.

(en.wikipedia.org/wiki/Mont_Saint-Hilaire)

(en.wikipedia.org/wiki/Mont-Saint-Hilaire,_Quebec)

The comparison of wetland and upland diversity in Quebec adds to my curiosity about the wetland-upland ecotones elsewhere. What is the overall contribution of the salt marsh-upland ecotone to the coastal plant diversity of southern California? What remains of that wetland-upland ecotone, and which species does it support—both plant and animal?

I hope readers will pursue further research in landscape diversity patterns, as well as the causes of species-rich and species-poor ecotones.