Welcome to the Conservation Lecture Series

www.dfg.ca.gov/habcon/lectures

Questions? Contact margaret.mantor@wildlife.ca.gov

Invasive *Spartina*
Ecological & Evolutionary Misadventures.

Donald Strong
Dept. Evolution and Ecology
&
Bodega Marine Lab
U C Davis

Credits to many who have worked on this project.

Special thanks to Debra Ayres who led the charge. She was the senior author of many publications on the story of creation, evolution, and invasion of hybrid *Spartina* in San Francisco Bay.

Strong, D. R. and D. A Ayres. 2013. Ecological and Evolutionary Misadventures of Spartina. Annual Review of Ecology, Evolution, and Systematics. Vol. 44. 389-410.

OUTLINE

I. Biology of Spartina

II. Introductions,

Invasions,

Hybridizations,

Evolution, &

Consequences.

=conservation et cet.

III. Control

← Native Atlantic

Native Pacific →

← Native Atlantic

Invaded Pacific →

Biology of *Spartina* 1

a. Grass

b. 13 Original species, in 1491.

11 New World, Atlantic natives.

1 Pacific, California cordgrass. *S. foliosa*.

1 Southern ocean sp. *S. arundinacia*.

Multiple Hybrid Species and Swarms.

c. No invasions or hybridizations

in central native range of western Atlantic.

d. Big invasions and hybridizations outside.

Biology of *Spartina* 2

d. A few species with huge influence,
ecological engineers,
aka “notorious invasive species.”

e. Evolution part and parcel of
invasion & hybridization.

*Wind pollinated, little or no selfing in nature.

! Hybrids evolve selfing !

Spartina spreads by seed
that floats on the tide.
No seed bank.

Spartina is an Ecological Engineer Native areas.

a. Builds intertidal lands with sediment trapping.

b. Very high primary and secondary productivity.

c. Sets species composition of plants and animals.

d. Base of elaborate food webs
nursery areas that extend far beyond estuaries.

Spartina is an Ecological Engineer Introduced areas.

a. Blocks upland drainage into estuaries.

b. Increases intertidal elevation and channelizes.

c. Changes species composition.

d. Environmental concerns:

conservation,

access to shore,

mariculture,

fishing,

navigation.

The potential to terrestrialize the shore was the rationale of many of the *Spartina* introductions,

Sediment Accretion, Organic Content, Channelization, &c.

From subtidal to intertidal: *Spartina alterniflora*, South Africa. 2010

New Zealand.

Early 20th century,
unabashed enthusiasm for introduced *Spartina.*

"For thousands of years tidal salt mud flats the world over have made entrances to harbours unsightly and treacherous and have remained as vast areas of waste flats… in the past they have provided an almost unconquerable challenge to man…Now such mud can be conquered, and …reclaimed to form useful and stable farmlands. This plant which has such an important role is …*Spartina townsendii*" (Harbord 1949).

Mid 20th C

A counterpoint of caution…

"Extensive areas of tidal flats round New Zealand's coastline, usually difficult and costly to develop, have become the subject of renewed interest with the introduction of the maritime grass *Spartina alterniflora*, which will enable many farmers to capitalize on these naturally fertile soils. … However, farmers are warned that the adverse influences may not always be readily apparent." (Blick 1965).

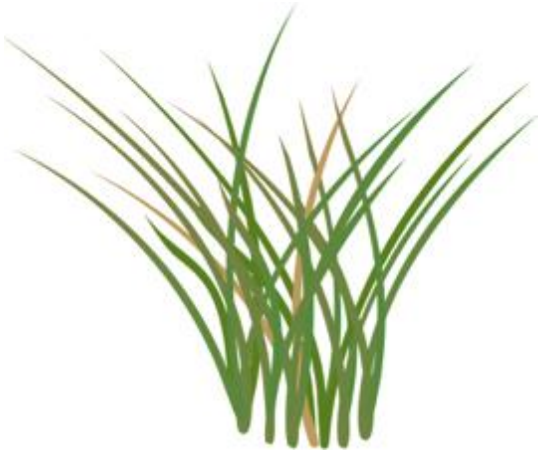
Last decades of the 20th C

Nuke it.

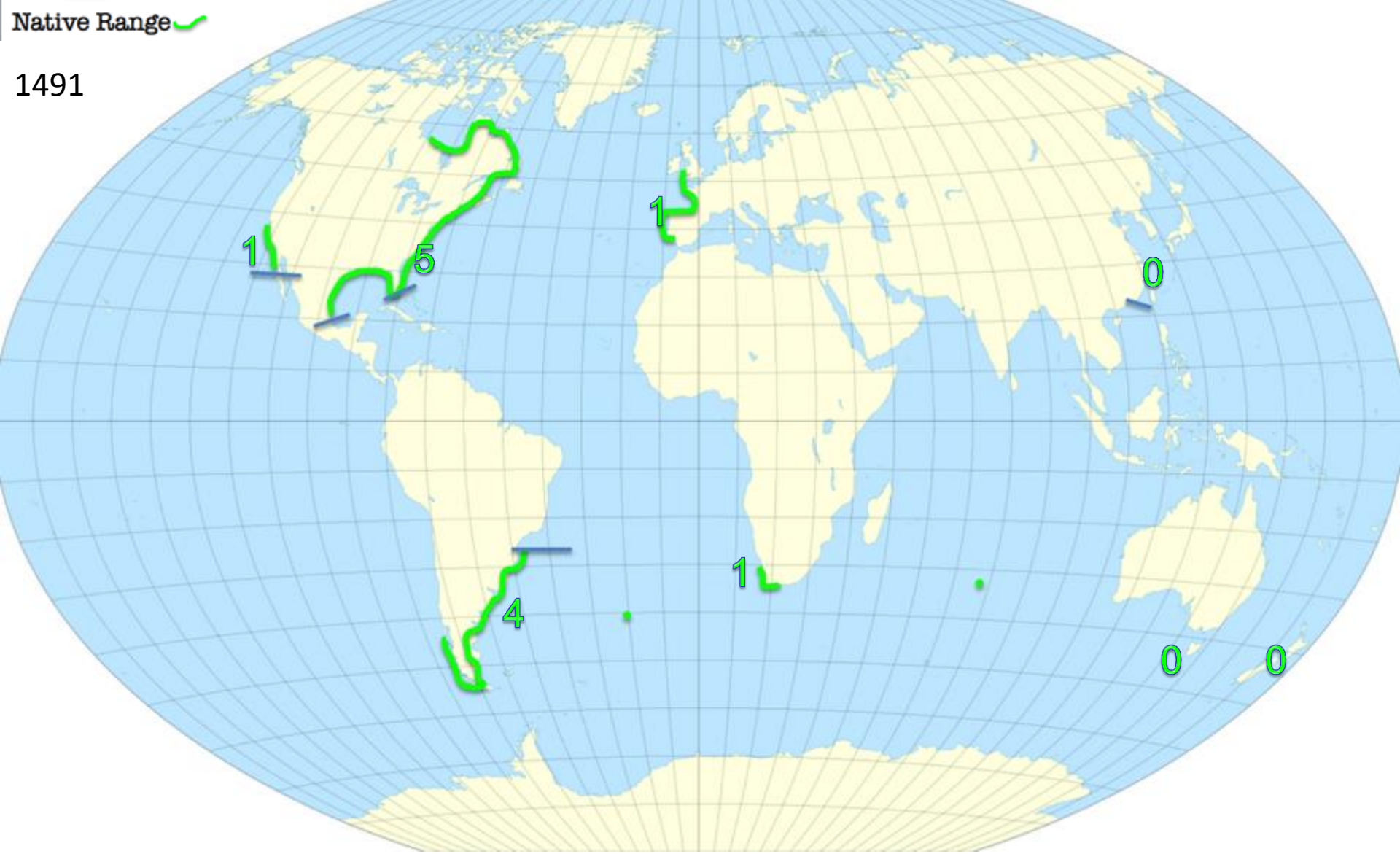
"In some places the problems caused by its spread are virtually insurmountable. With renewed appreciation of estuarine wetlands in their natural states, planting of any species of *Spartina* around the coast of New Zealand should not be allowed to take place. Suitable control and eradication measures need to be developed where *Spartina* is already present" (Partridge et al 1987).
New herbicides and new methods of application have eradicated all meadows and patches of *S. anglica* in South Island (Miller 2004).

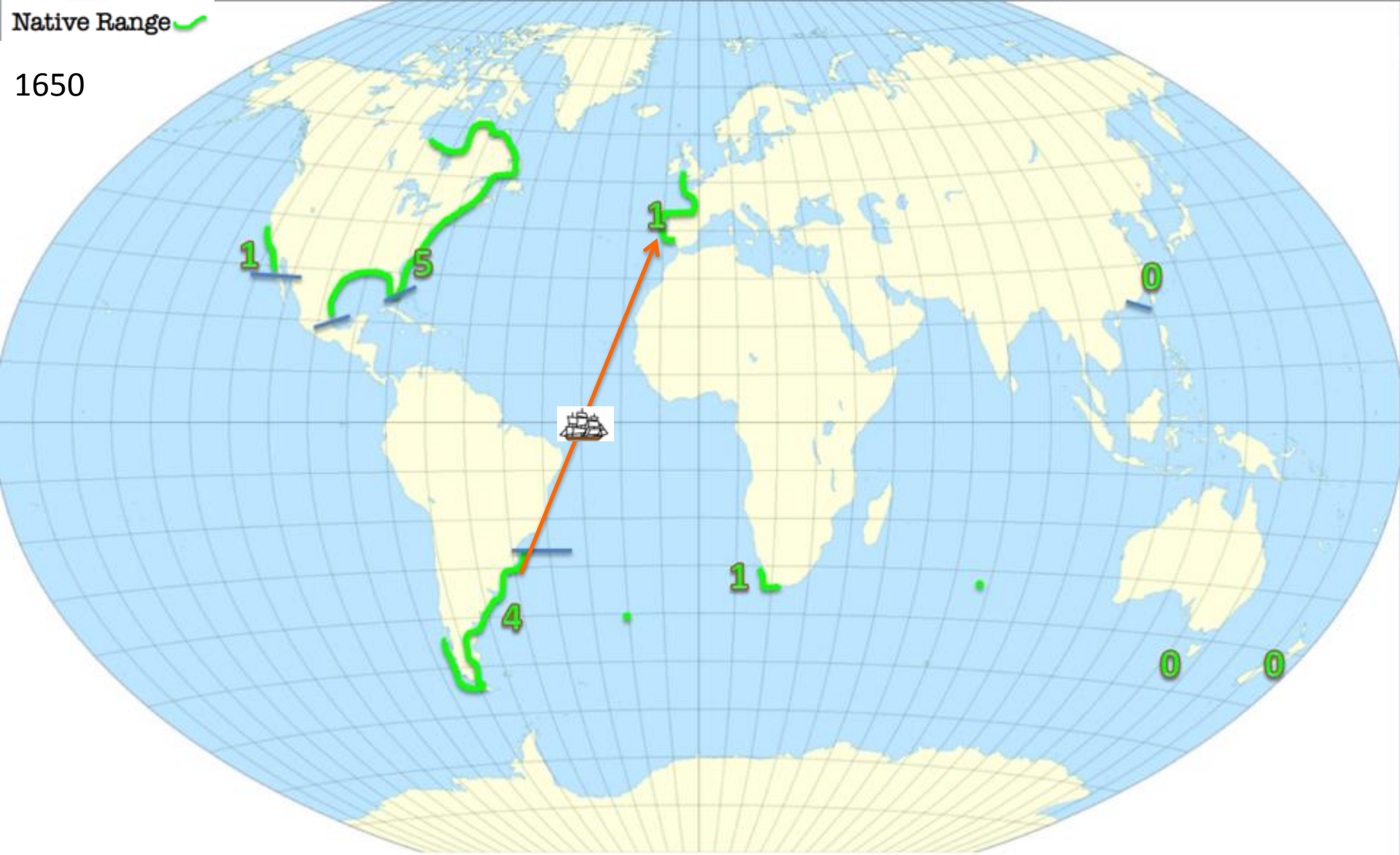
The changing attitudes of society are reflected in the ethos, motivations, and endeavors of those concerned with the environment.

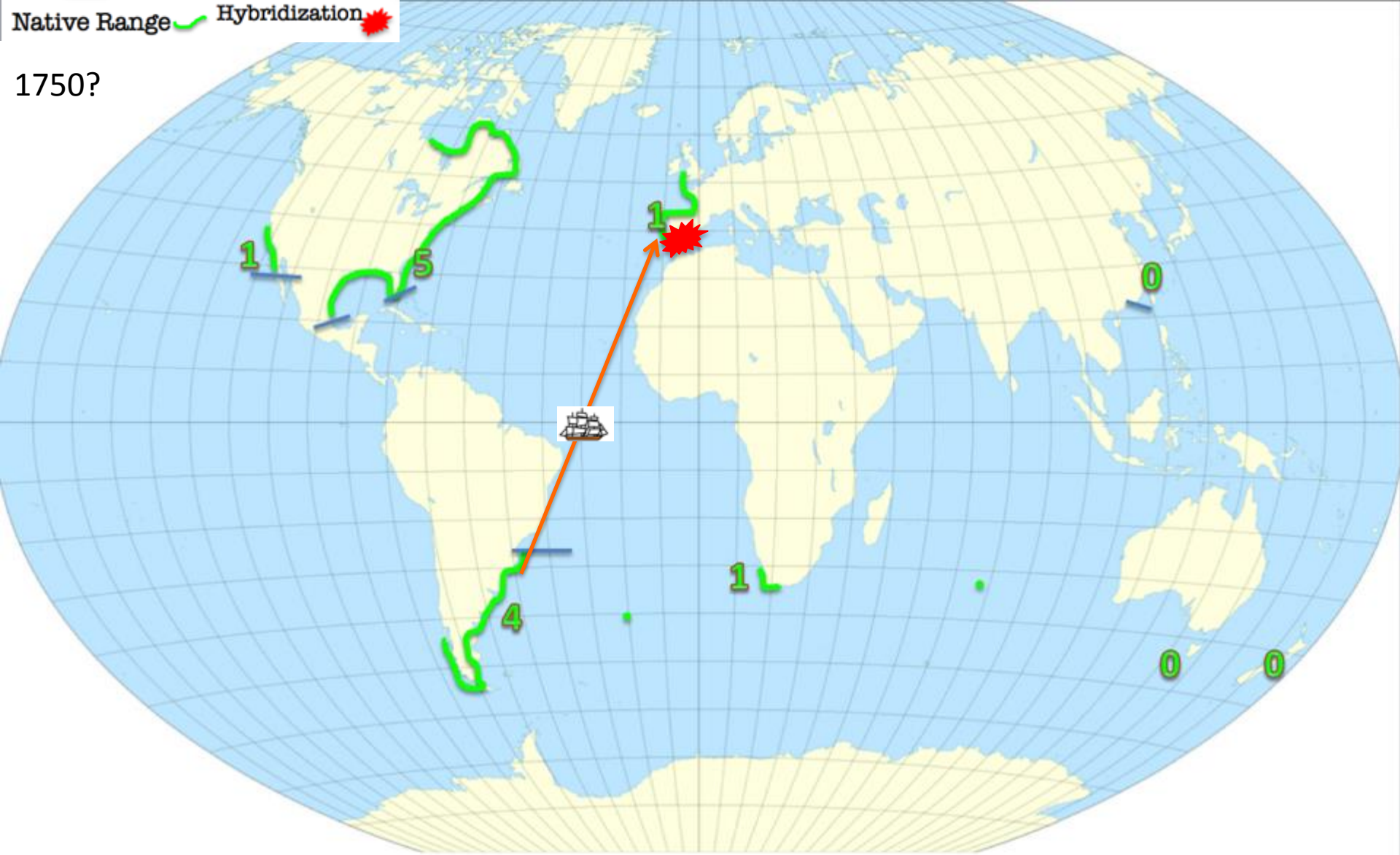
Spartina illustrates these changes.

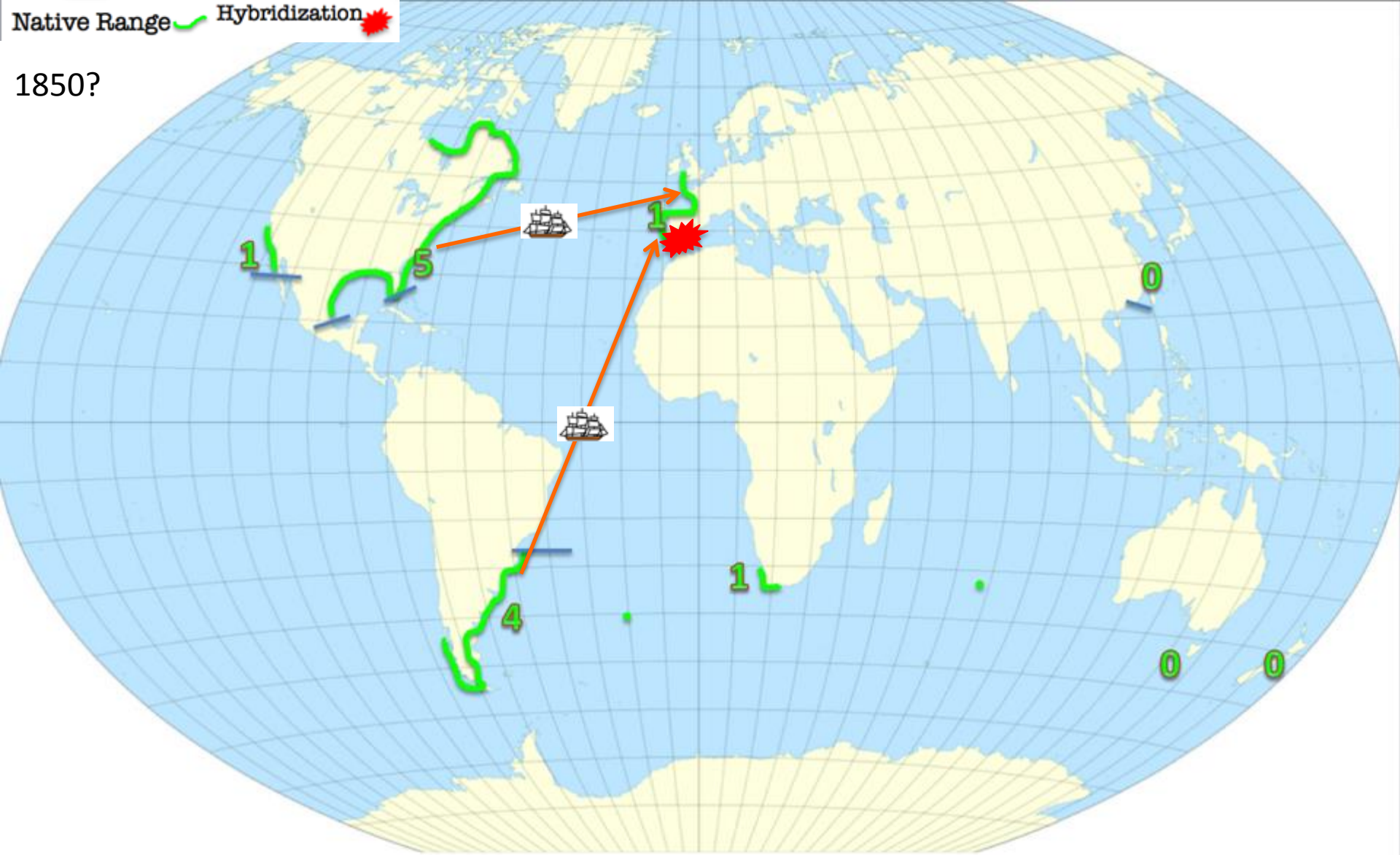


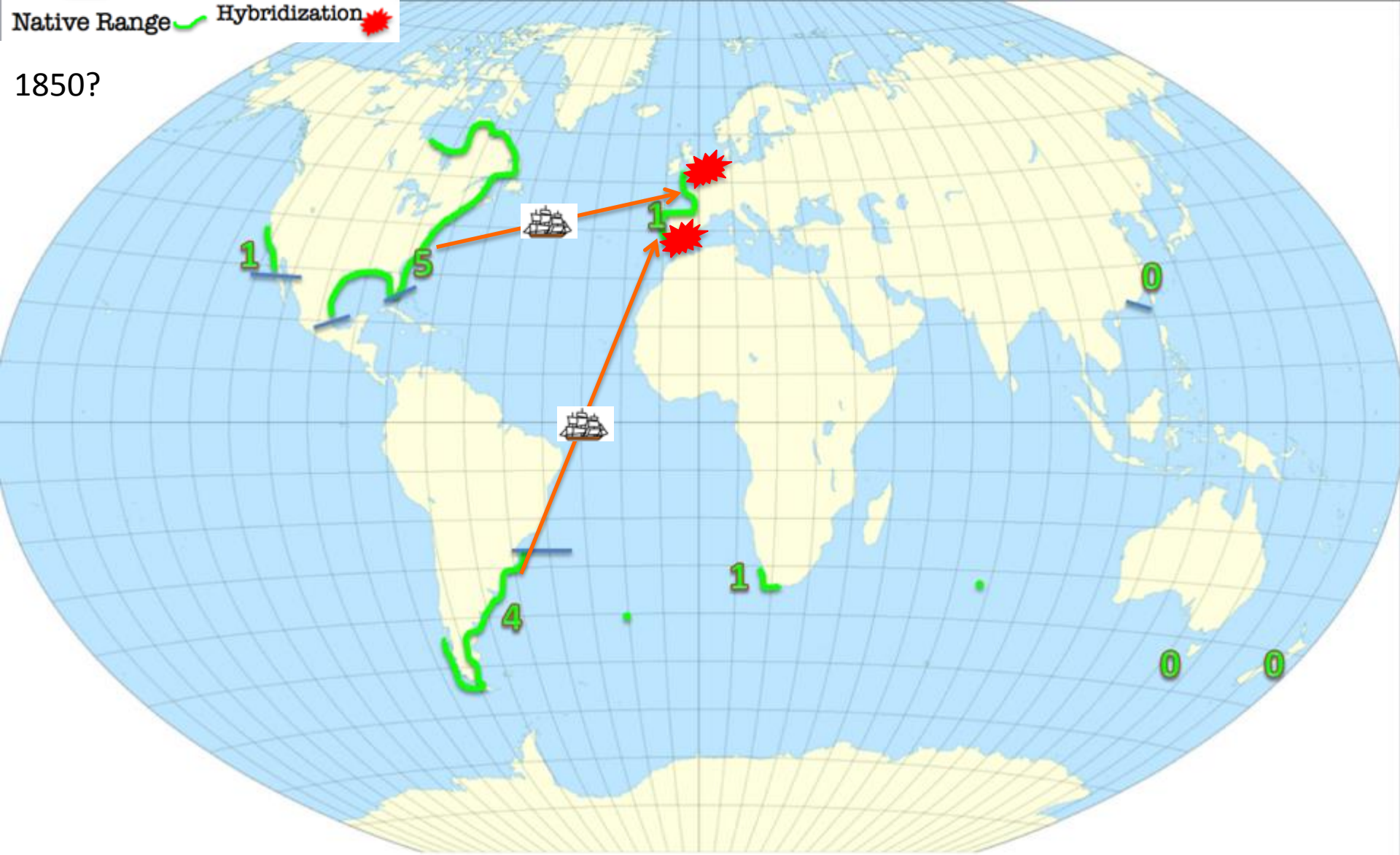
Strong, Ayres, & Feinstein. In prep. The Ecological and Evolutionary Misadventures of Invasive Spartina. *Ann. Rev. Ecol, Evol. & Syst.*

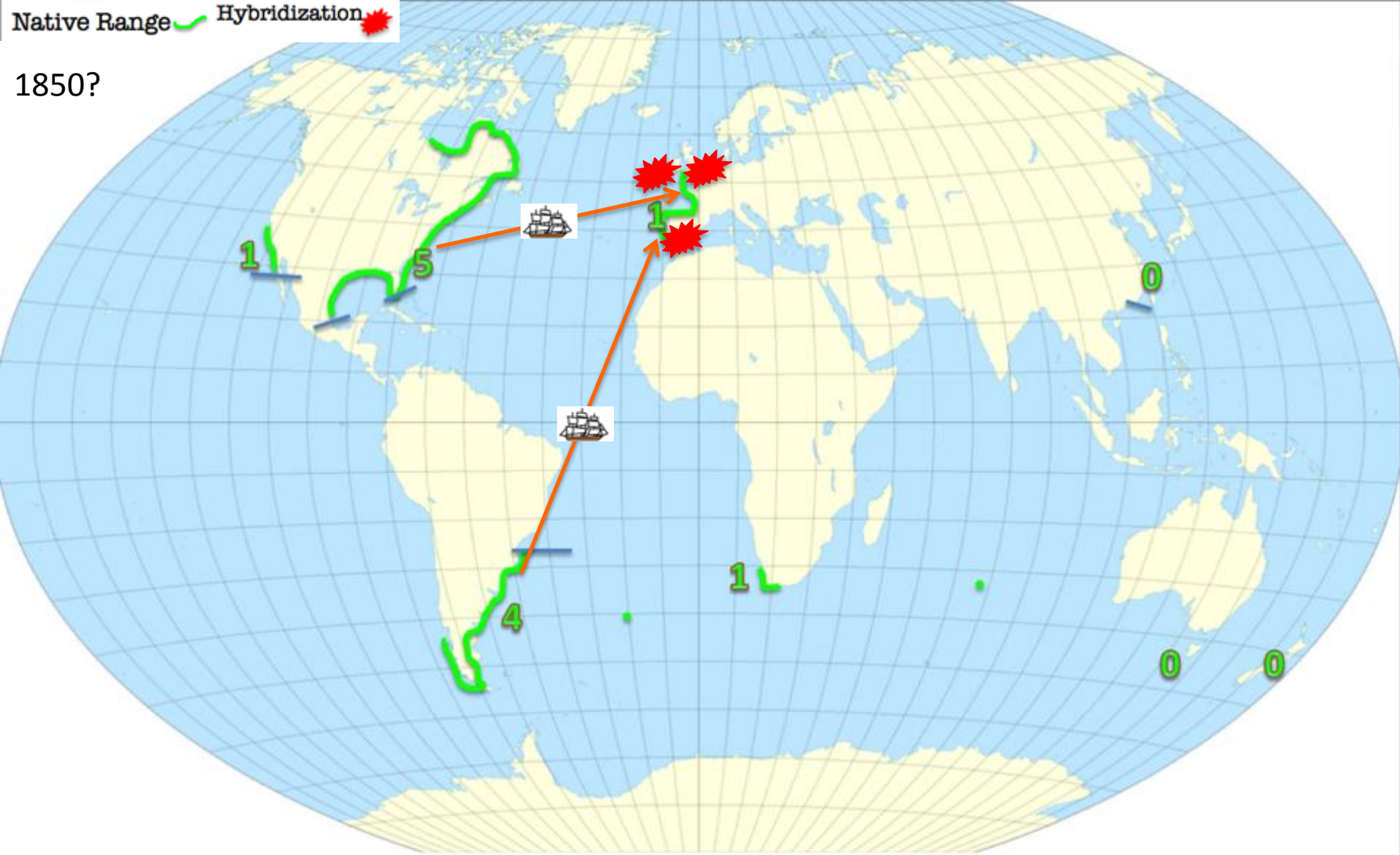

Native Range
1491
1
5
1
0
1
4
0
0

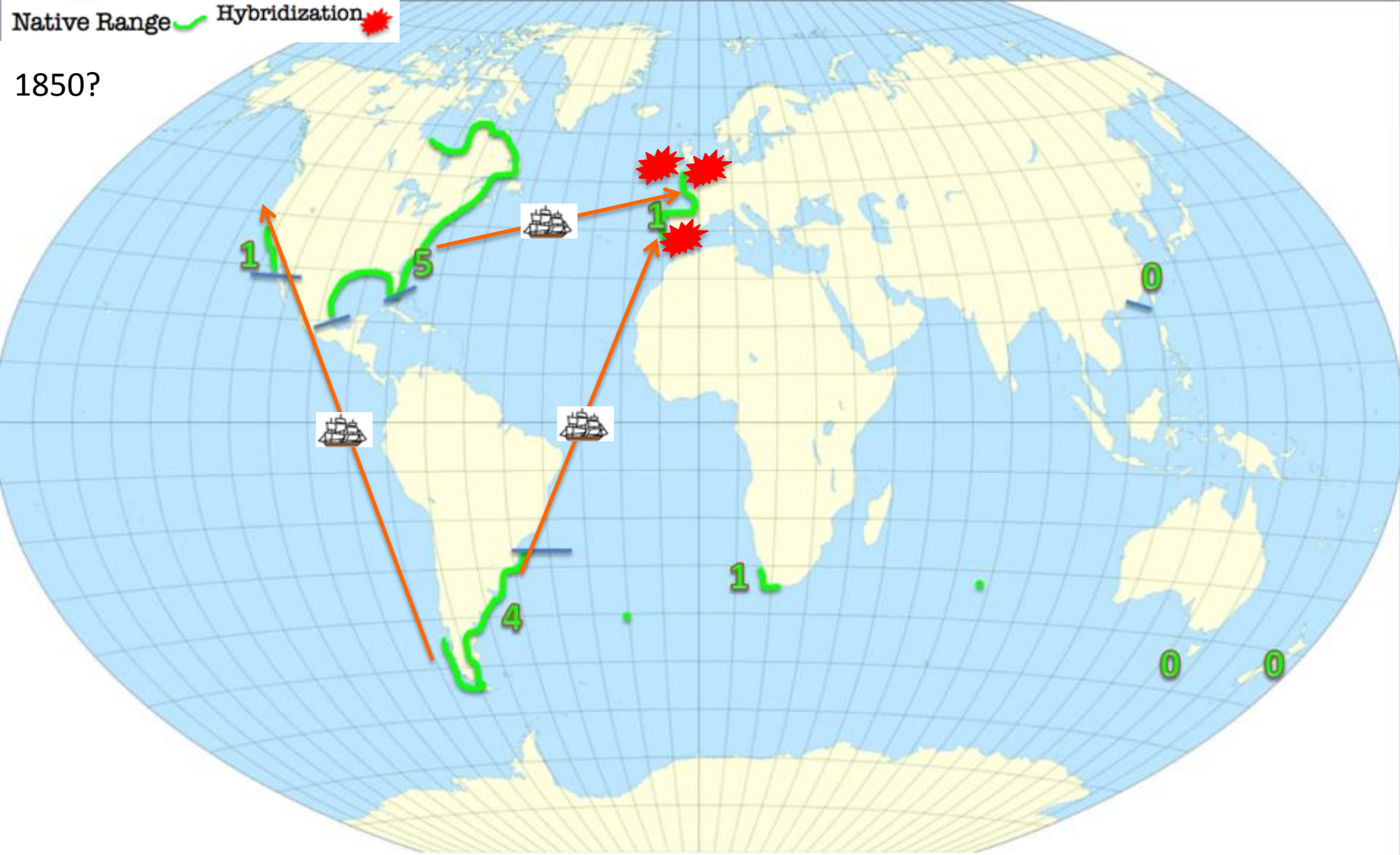

Native Range
1650
1
5
1
0
1
4
0
0

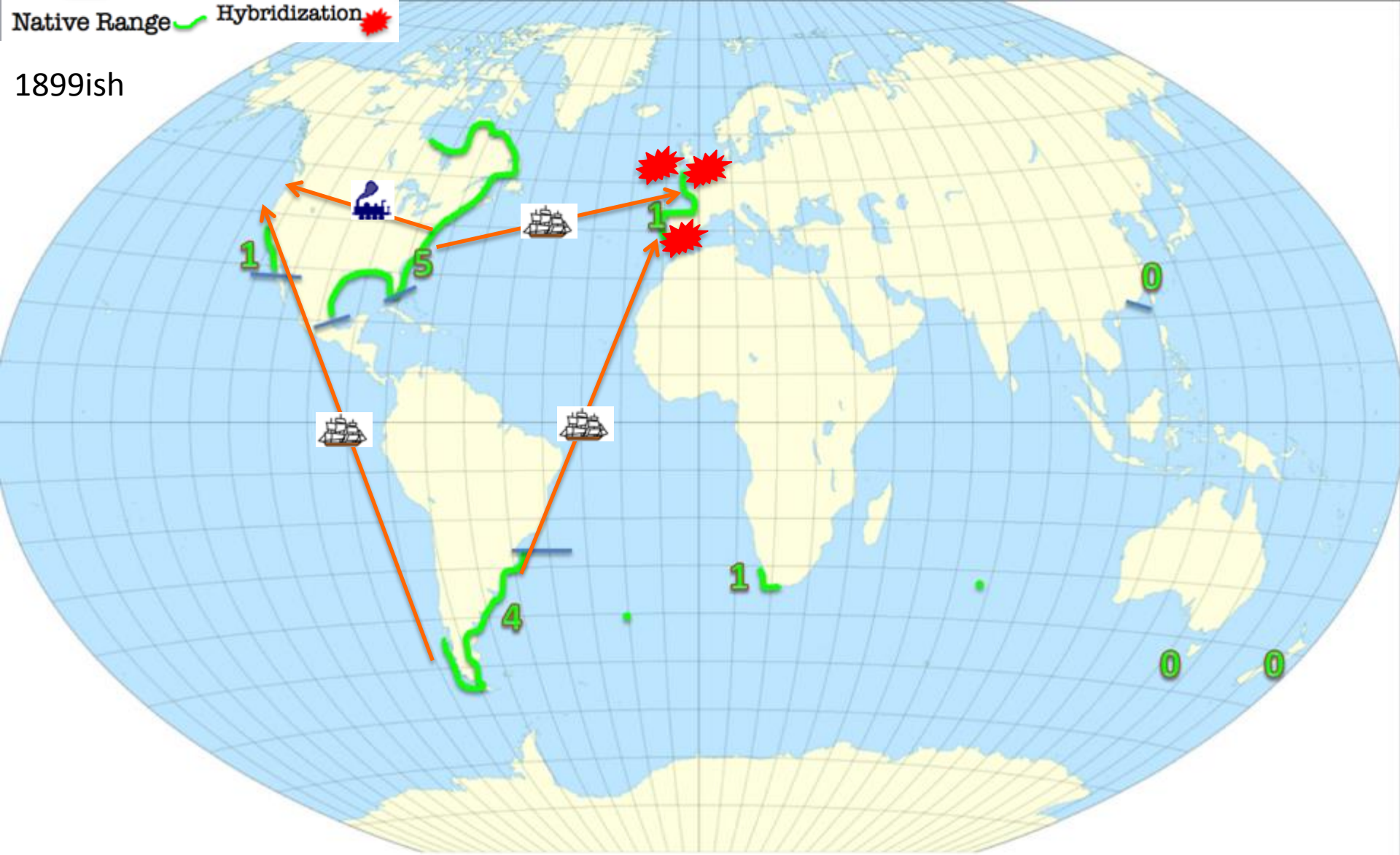

Native Range
Hybridization
1750?
1
5
1
1
4
0
0
0

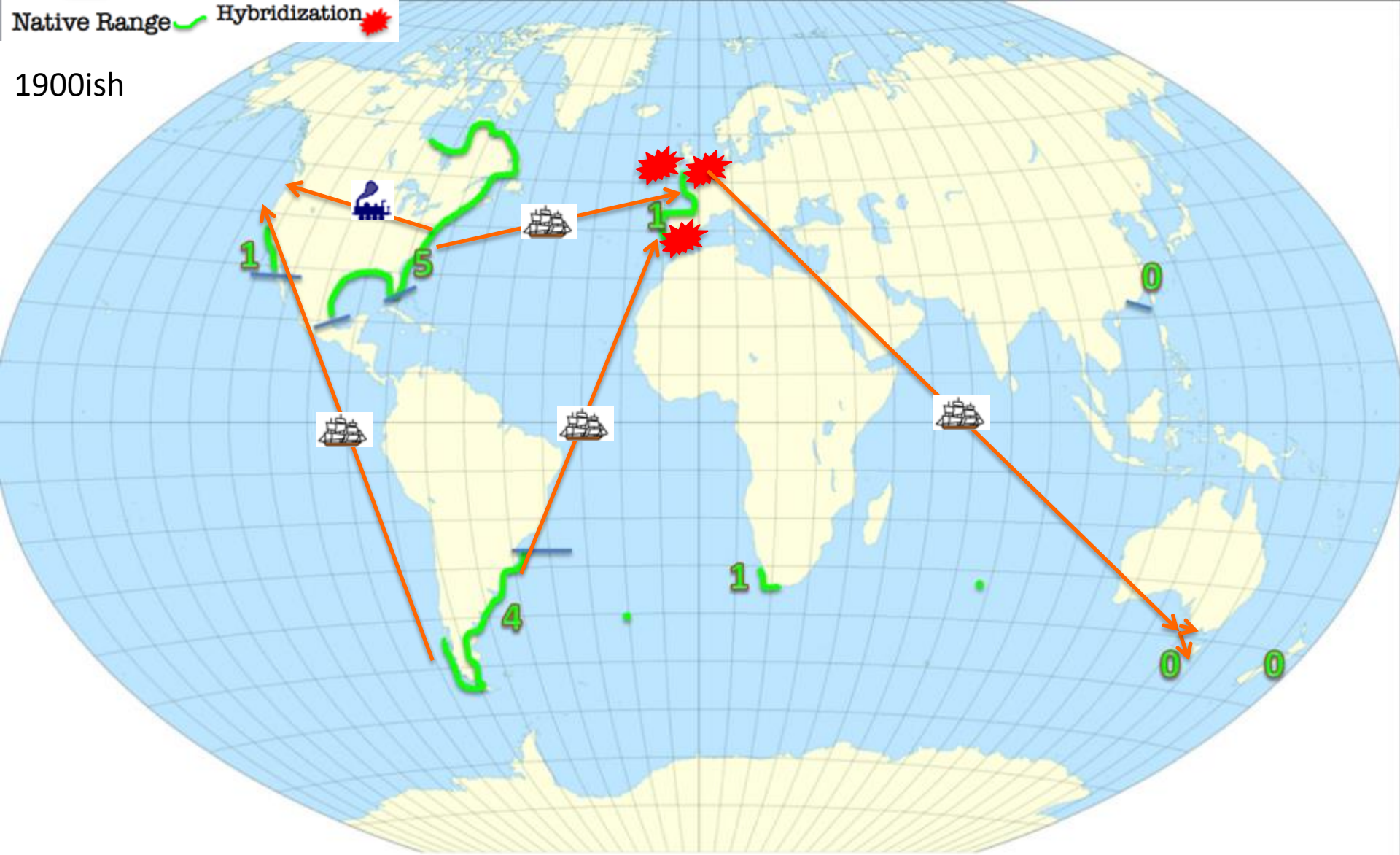

Native Range
Hybridization
1850?
1
5
1
0
1
4
0
0

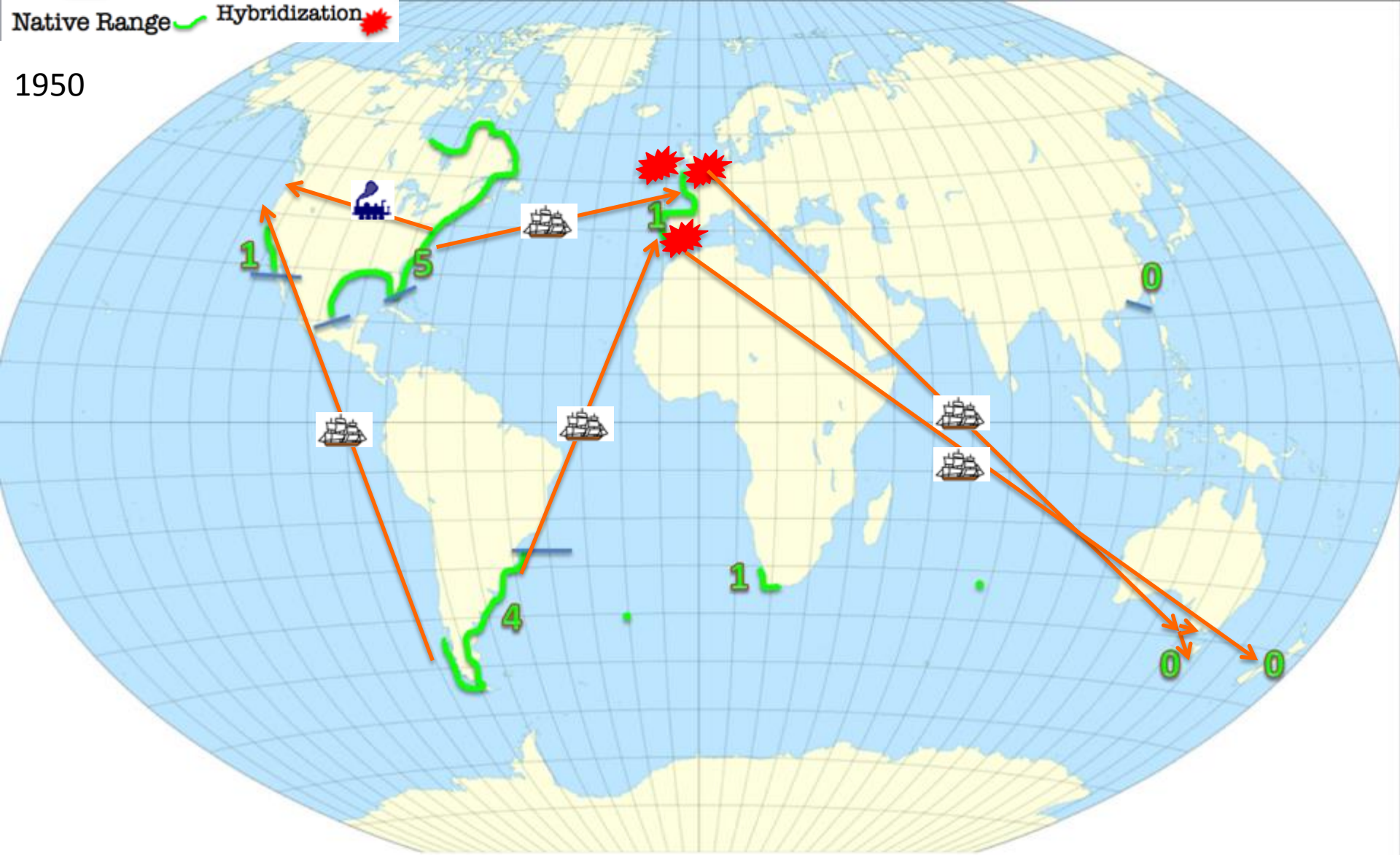

Native Range
Hybridization
1850?
1
5
1
0
1
4
0
0

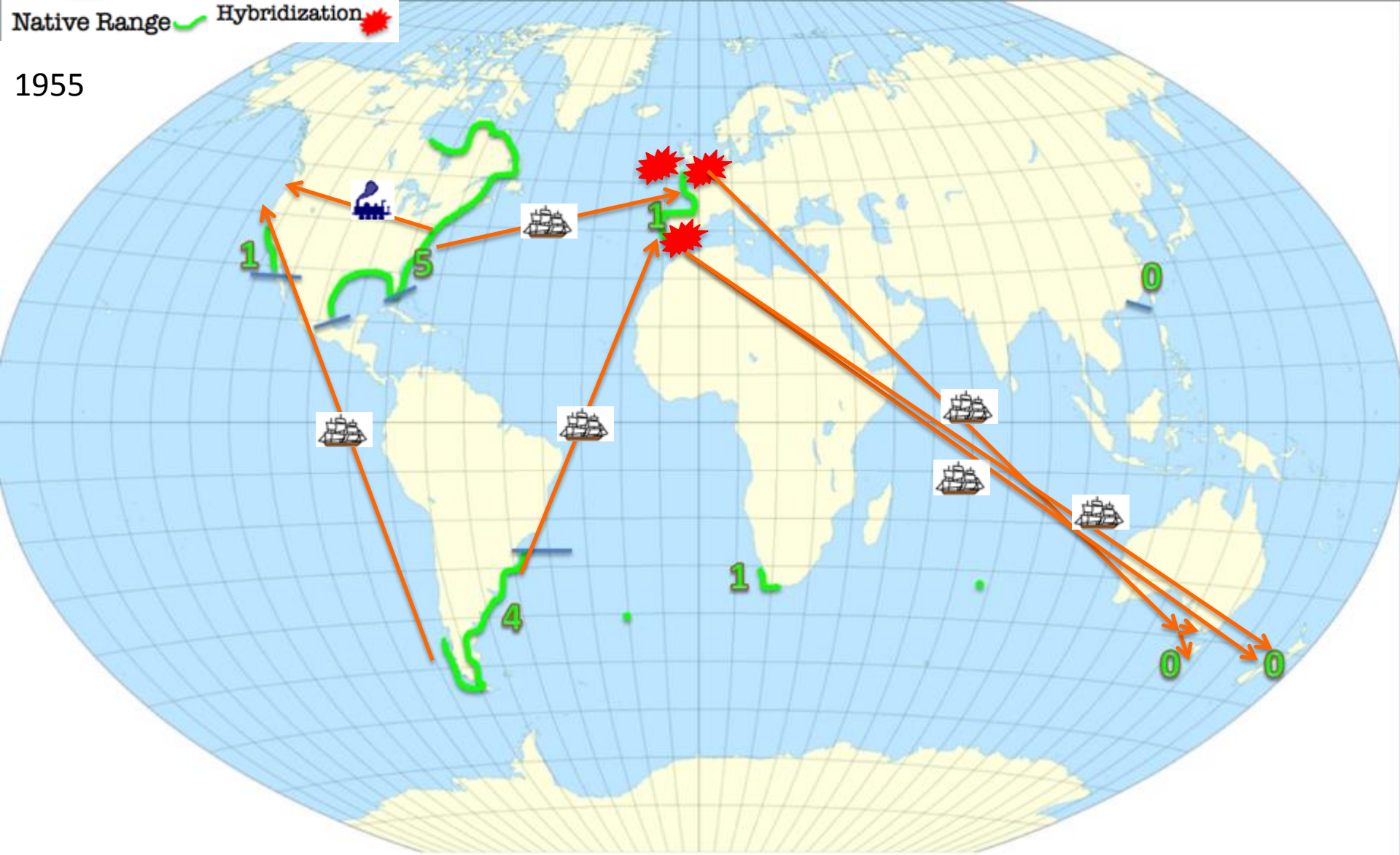

Native Range
Hybridization
1850?
1
5
1
0
1
4
0
0

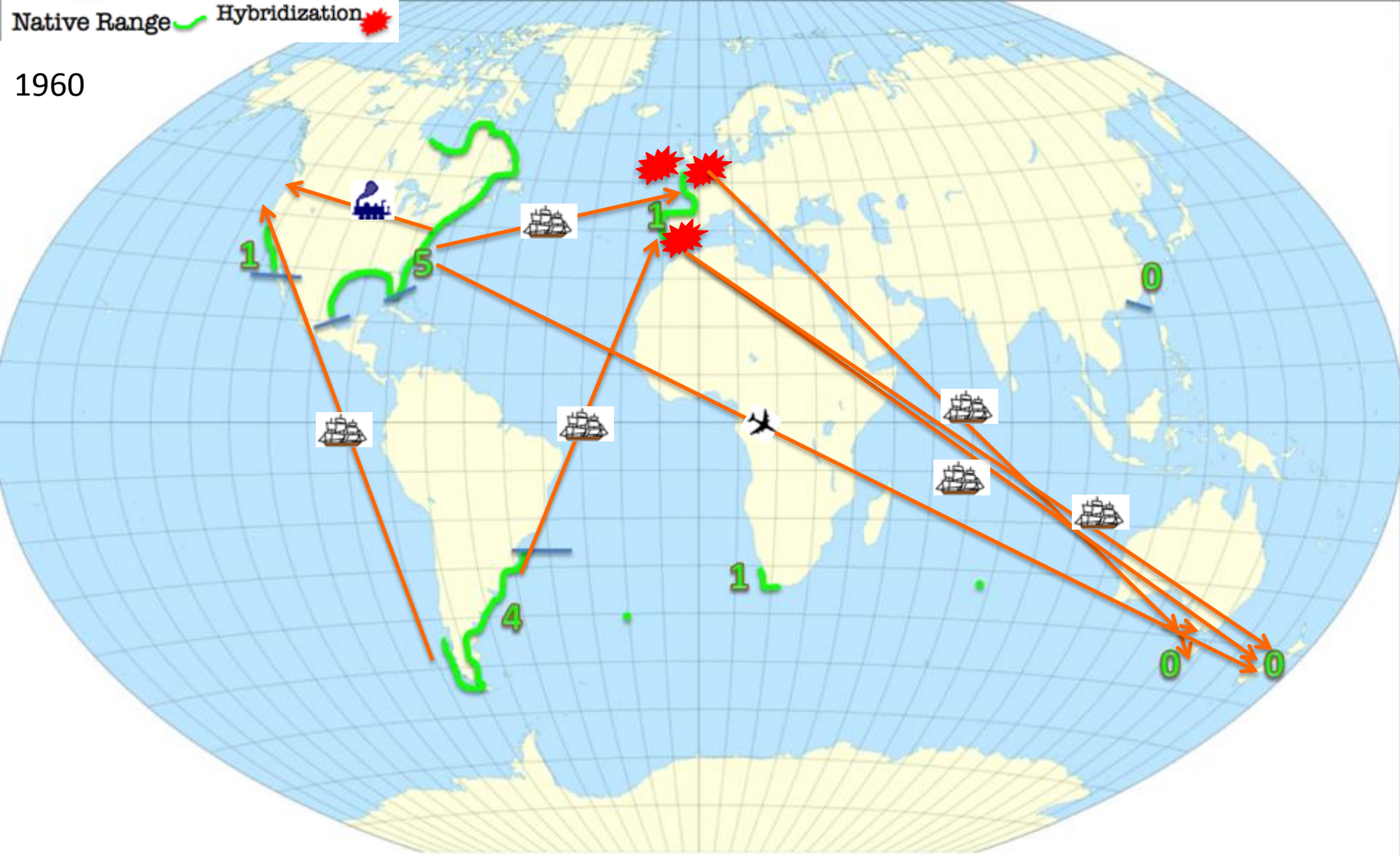

Native Range
Hybridization
1850?
1
5
1
0
1
4
0
0

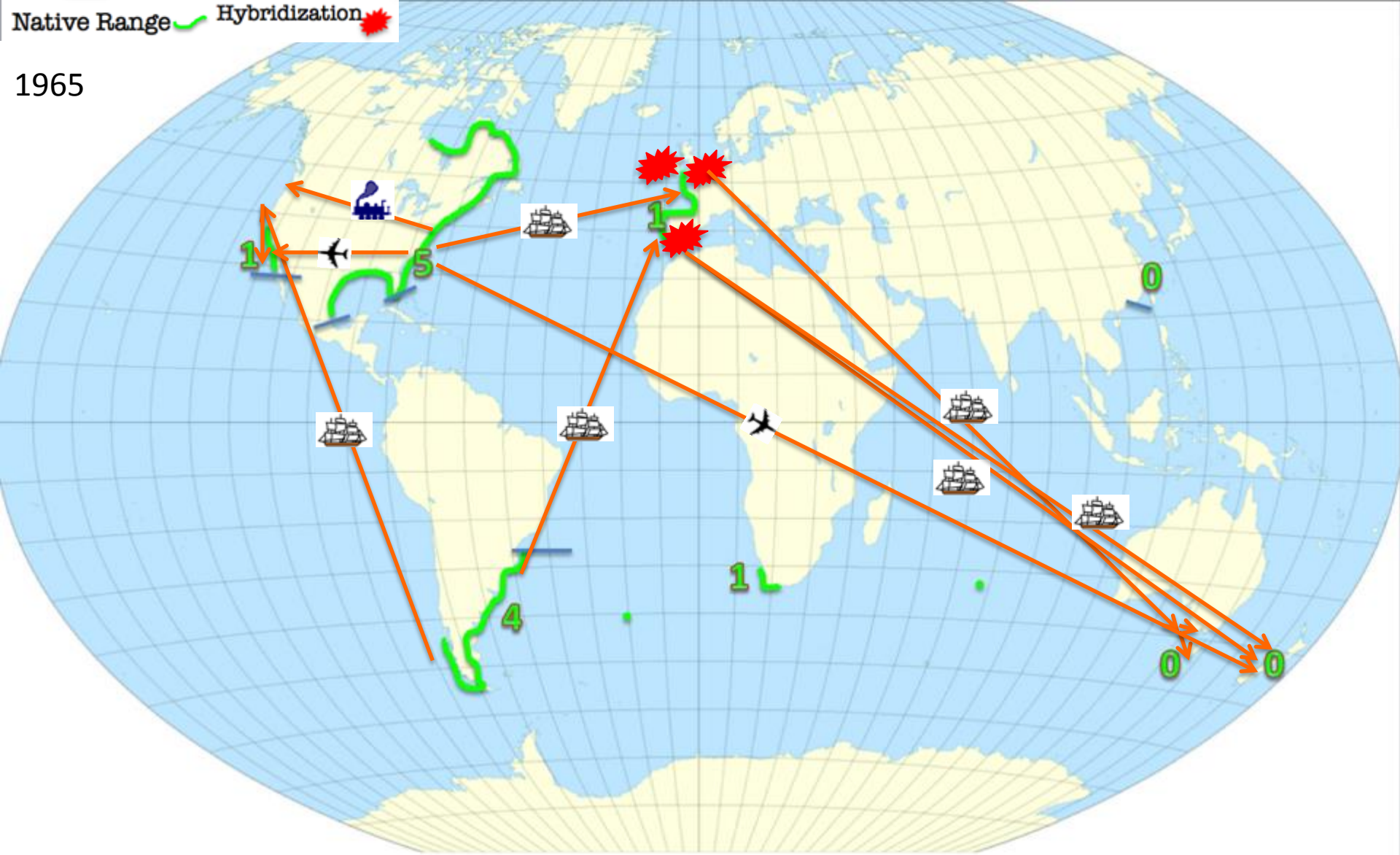

Native Range
Hybridization
1899ish
1
5
1
0
1
4
0
0

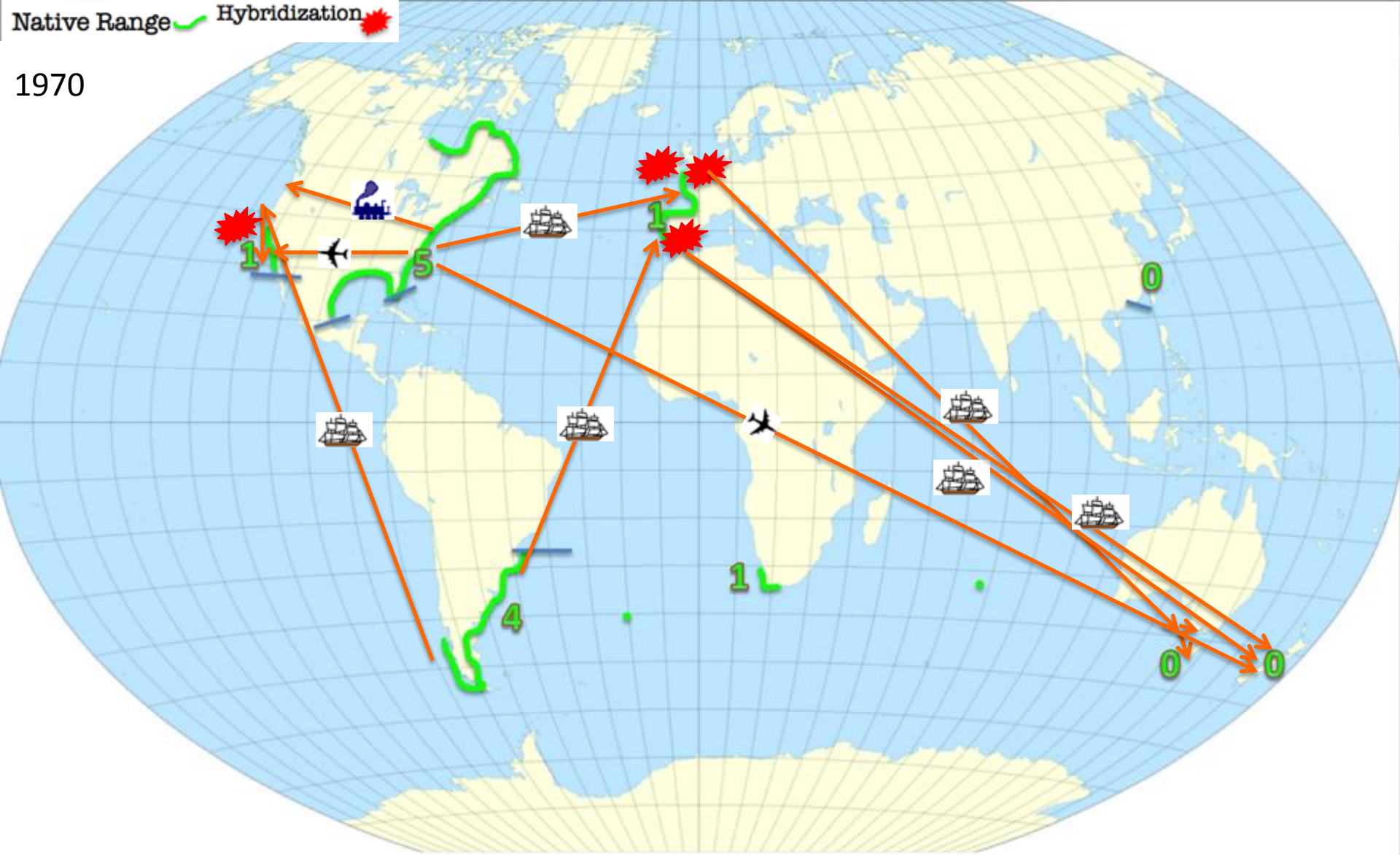

Native Range
Hybridization
1900ish
1
5
1
0
1
4
0
0

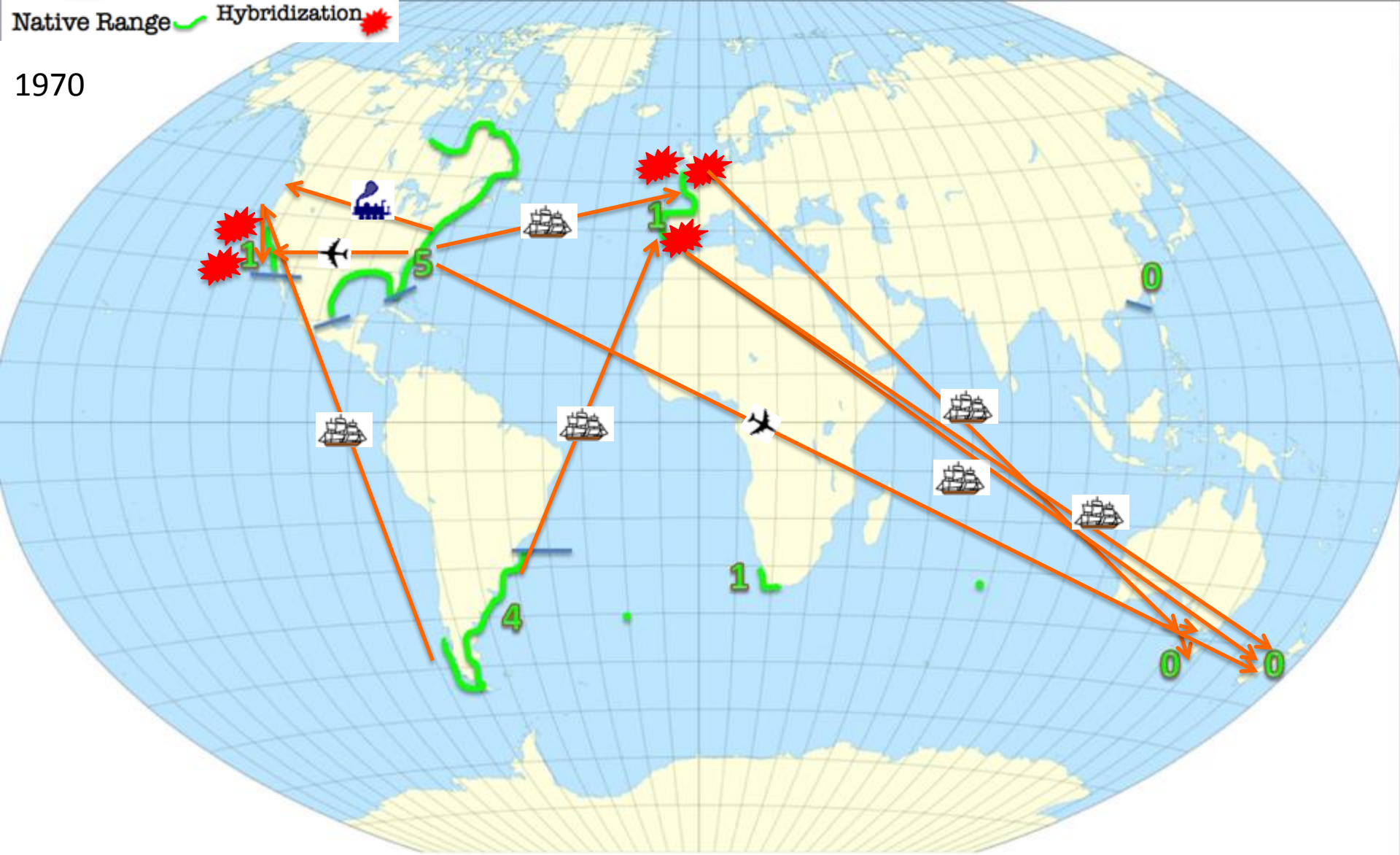

Native Range
Hybridization
1950
1
5
1
0
1
4
0
0

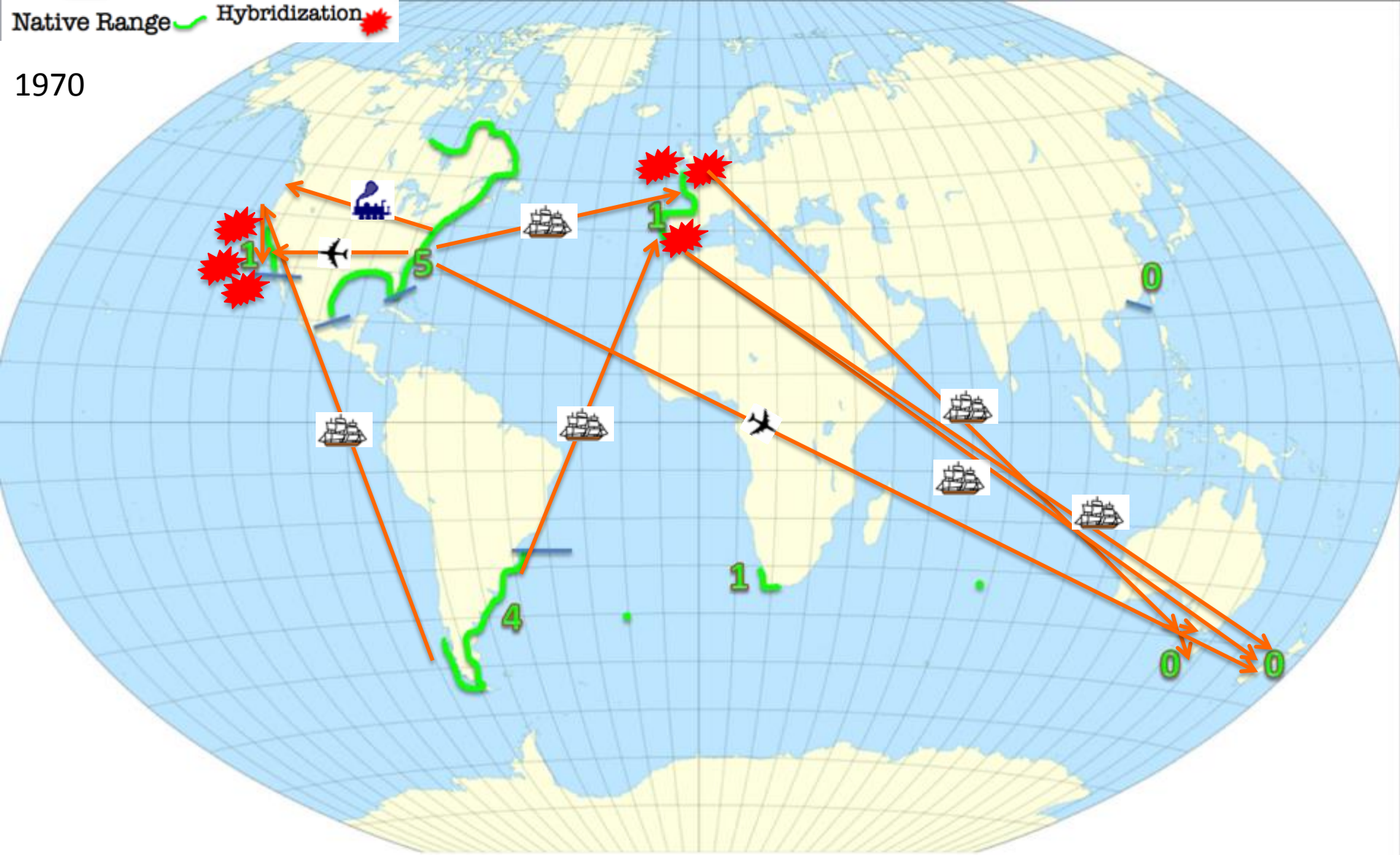

Native Range
Hybridization
1955
1
5
1
0
1
4
0
0


Native Range
Hybridization
1960
1
5
1
1
4
0
0
0


Native Range
Hybridization
1965
1
5
1
0
1
4
0
0


Native Range
Hybridization
1970
1
5
1
1
4
0
0
0


Native Range
Hybridization
1970
1
5
1
1
0
4
0
0


Native Range
Hybridization
1970
1
5
1
0
1
4
0
0

The San Francisco Estuary.

- 70% of the mudflats in California.
- 1 million migrating shorebirds in fall, Second only to Alaska in importance to Pacific coast flyway.
- Western Hemisphere Shorebird Reserve Network (WHSRN)
- Highest possible ranking.

Open Intertidal Mud & Native *Spartina foliosa*

- Shorebird feeding areas.

Dense, tall Hybrid *S. foliosa* x S. *alterniflora*.

- Excludes shorebirds.

Herbicide campaign

- against hybrid *Spartina.* 2001-2010.
- Successful for shore birds, cleared intertidal

Complications, California clapper rail = Ridgeway rail).

Hybrid *Spartina* is a threat to migratory shore birds in SF estuary.

San Francisco Estuary.

Spartina alterniflora introduced by Army Corps of Engineers, ca 1970.
Native California cord grass, *Spartina foliosa*
hybridized with S*. alterniflora* soon thereafter.

S. alterniflora

S. foliosa

Hybrid
S. alterniflora
x
S. foliosa

Ayres, D. A & al. many publications from 1999 ..

Ridgeway rail populations,

declined drastically in the first half of the 20th century:
hunting, egg collecting, loss of saltmarsh habitat to agriculture and urbanization,

extinct in all estuaries except SF Bay,

began to recover in habitat provided by the tall hybrid *Spartina* that spread across SF Bay after the 1970's,

densest in hybrid *Spartina* in San Francisco Bay.

Herbicide treatment between 2005 and 2011 widely removed hybrid *Spartina* from intertidal mud and preserved habitat of shorebirds.

However, removal of hybrid *Spartina* caused substantial decreases in rail populations. Loss of cover and loss of refuge from predators.

*Hybrid Spartina created a refuge for the Ridgeway rail,

an endangered species.

*Fewer than 2000 remain.

*They thrive in hybrid *Spartina*,

and disappear from areas where hybrid *Spartina* has been killed.

Ridgeway Rail Refuge disappears at king tide. China Camp. No hybrid Spartina.

Controlling Invasive S*partina*

The herbicide campaign removed hybrid *Spartina* from large sections of the San Francisco estuary.

Figure 10e. This northwest facing photo of Dog Bone Marsh shows the high success of hybrid *Spartina* treatment at the site.

Cory Overton

Toby Rohmer

Ridgeway rail **survival**
+73% in hybrid *Spartina* areas
before herbicide killing than after.

Similar differences:
before herbicide hybrid
v.
native S. foliosa (not sprayed).

Overton et al. (2014). "Tidal .. survival rates …endangered California clapper rail.. Biological Invasions 16(9): 1897-1914.

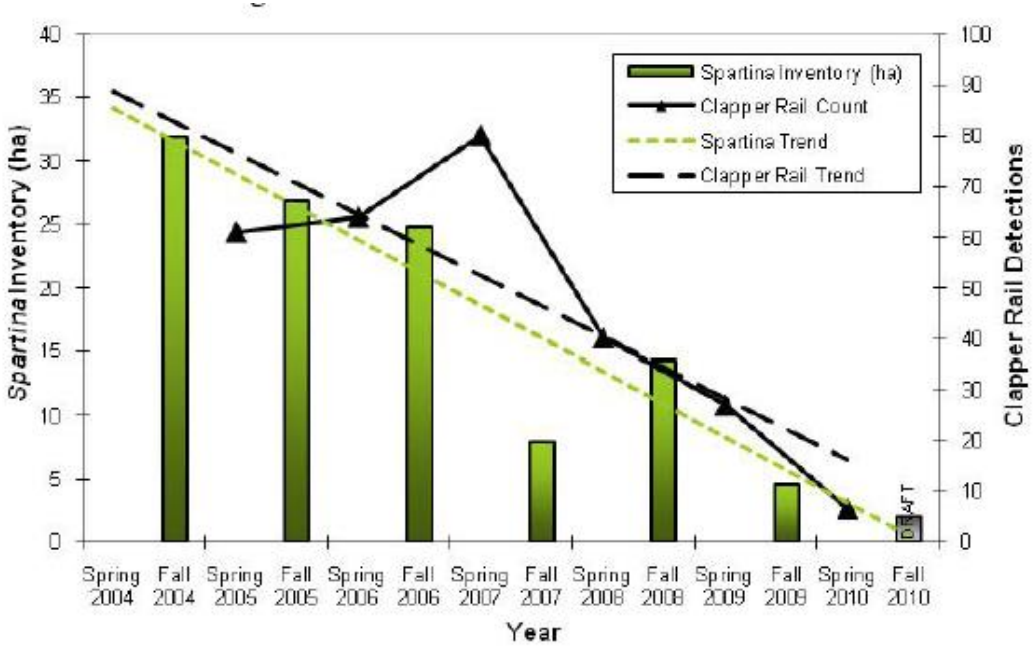
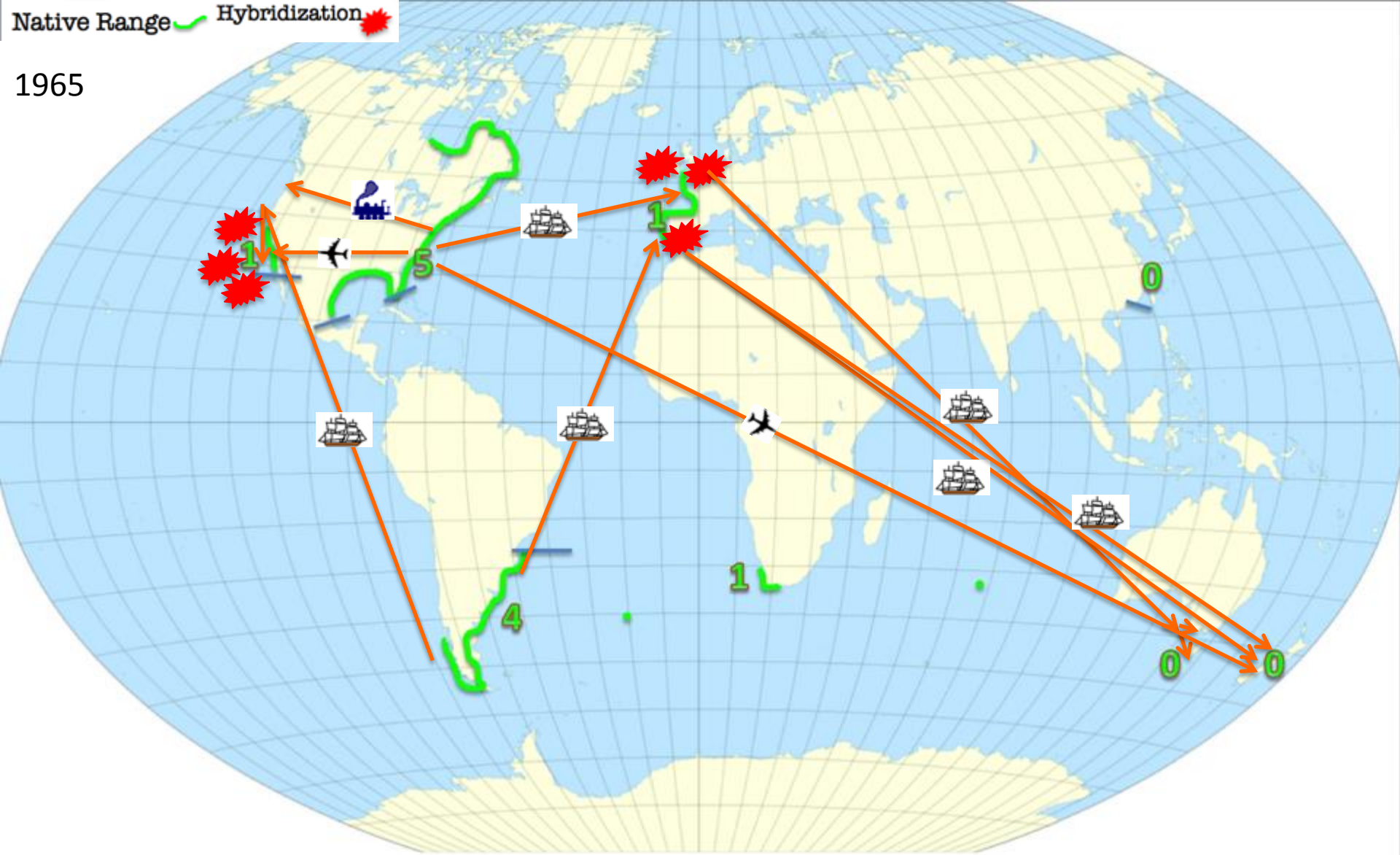
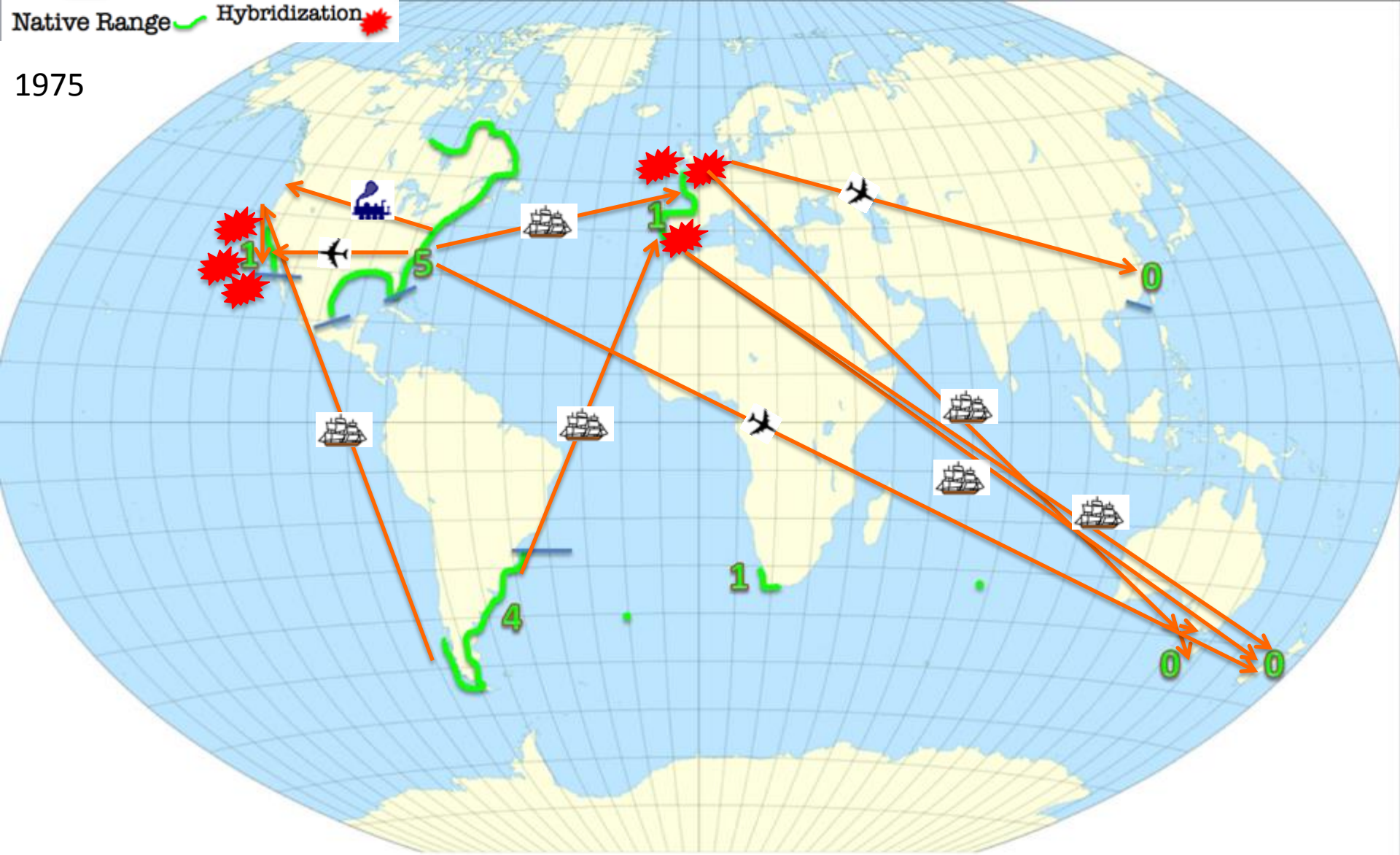
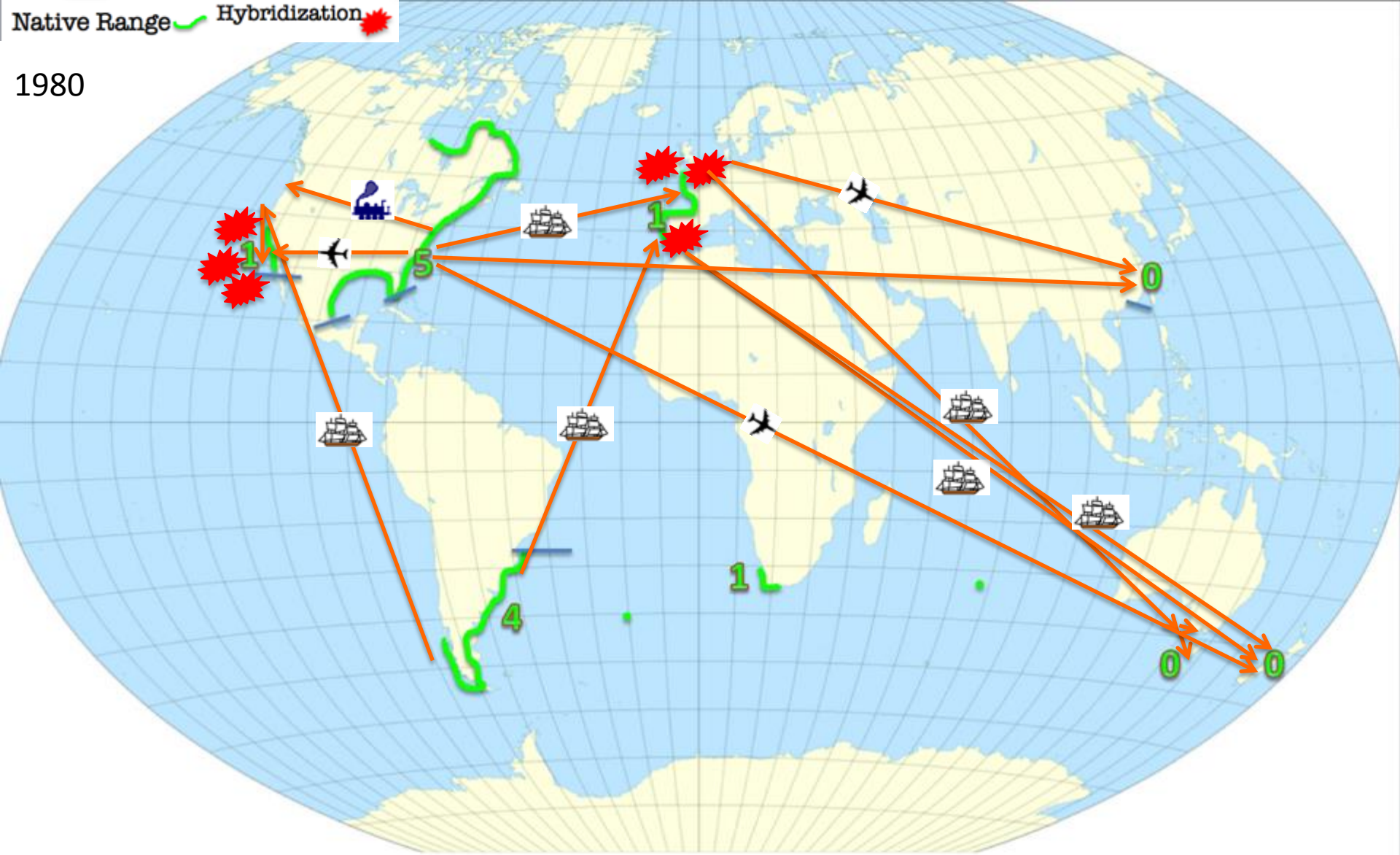


Figure 39. Annual Inventory of *Spartina* and Clapper Rail Populations in the San Francisco Peninsula Region (n = 8 sites)

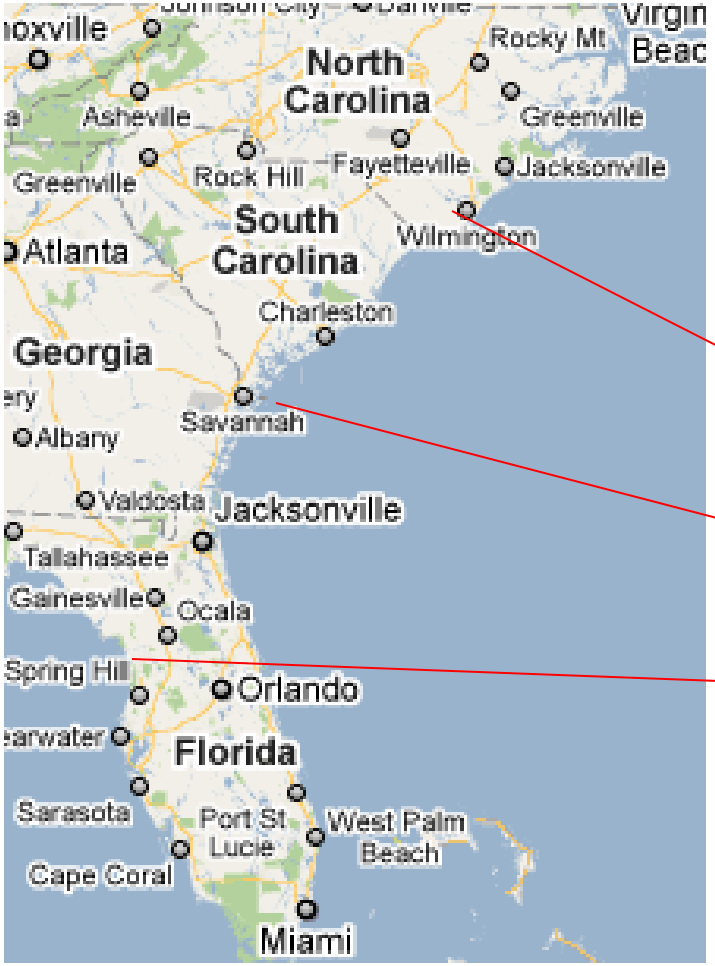
Invasive Spartina Project 2010 Survey Report.


Native Range
Hybridization
1965
1
5
1
0
1
4
0
0


Native Range
Hybridization
1975
1
5
1
0
1
4
0
0


Native Range
Hybridization
1980
1
5
1
0
1
4
0
0

1979. *Spartina alterniflora* from Georgia, Florida & North Carolina.
Introduced to Luo Yuan Bay, Fujian Province, China.
Planted out, selected big, fast growers, which were spread widely.
Some of this S. alterniflora grows to huge stature.
Crossed or breeding pattern? Selfing?



Mariculture, mangrove conservation, & *Spartina* invasion on the most intensively farmed coastline in the world. Spartina was introduced to this area **only a decade ago.**

Zhangjiang Estuary, Fujian Province, China
Supertidal: rice and vegetables.
Intertidal: clams, crabs, oysters.
Attempts at mangrove conservation.

Typhoon Prapiroon
Oct 18, 2012

Mariculture channels

Razor clam industry, Zhangjiang Estuary, Fujian Prov. ,China


GIANT

Zhang, Y. H., et al. (2012). "Interactions between mangroves and exotic Spartina in an anthropogenically disturbed estuary in southern China." Ecology 93(3): 588-597.

Invasive *Spartina alterniflora* & south China Razor Clam Industry

http://chinaspartina.blogspot.com

Spartina Research in the Salt Marsh Lounge

Debra Ayres

Carina Anttila-Suarez

Katy Zaremba

Dino Garcia Rossi

Mary Packenham-Walsh

John Lambrinos

Laura Feinstein

Curt Daehler

Heather Davis

Janie Civille

Christina Sloop

Mike Blum

Caz Taylor

Toby Rohmer

Jun Bando, Richard Hall, Cory Overton, Renate Eberl

support: BML, UCD, Invasive Spartina Project of California Coastal Conservancy, NSF, California Sea Grant, State of Washington, Washington Sea Grant &c.

Spartina Research in the Salt Marsh Lounge

Debra Ayres

Carina Anttila-Suarez

Katy Zaremba

Dino Garcia Rossi

Mary Packenham-Walsh

John Lambrinos

Laura Feinstein

Curt Daehler

Heather Davis

Janie Civille

Christina Sloop

Mike Blum

Caz Taylor

Toby Rohmer

Jun Bando Richard Hall Cory Overton Renate Eberl

support: BML, UCD, Invasive Spartina Project of California Coastal Conservancy, NSF, California Sea Grant, State of Washington, Washington Sea Grant &c.

Original Species

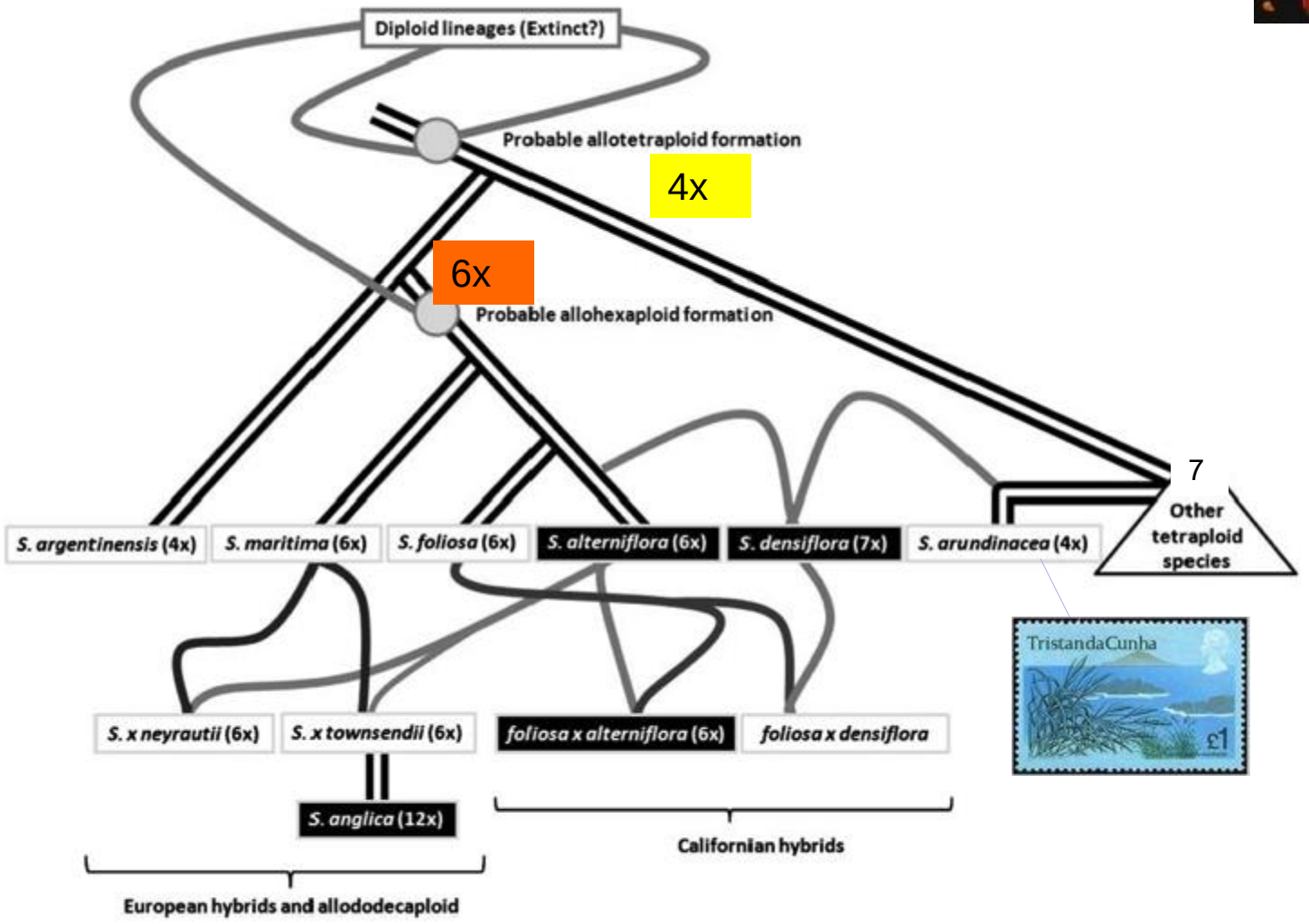
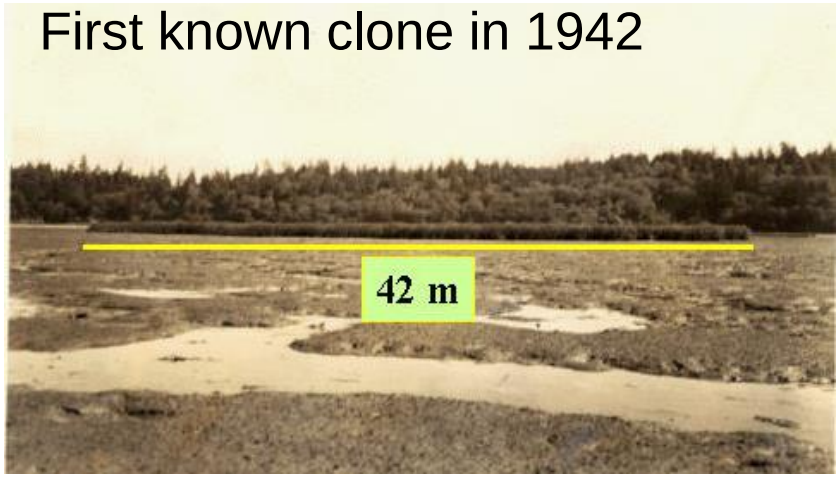


Fig. 3 Divergent (*straight lines*) and reticulate (*curved lines*) phylogenetic relationships in genus *Spartina*. *Filled boxes* indicate notorious invasive species

Ainouche & al. 2009. Hybridization, polyploidy and invasion: lessons from Spartina (Poaceae). *Bio. Invas.* **11**(5): 1159.

Hind casting to the origin of the invasion



Clone growth rates of thousands distinct clones from 1994, 1997, 2000 from Janie's GIS of remote sensed data

Mean increase in radius of 1.56 m/3yr.

Diameter of first known clone in 1942 = 42 m.

Hind cast of birth date of first clone:

$3(42)/[2(1.56)] = 40.4$ yr. $\quad 1942 - 40.4 \cong 1902$ +/- a few mos.

Dennis & al. 2011. Lateral spread of invasive Spartina alterniflora in uncrowded environments. *Bio. Invas.* 13(2): 401

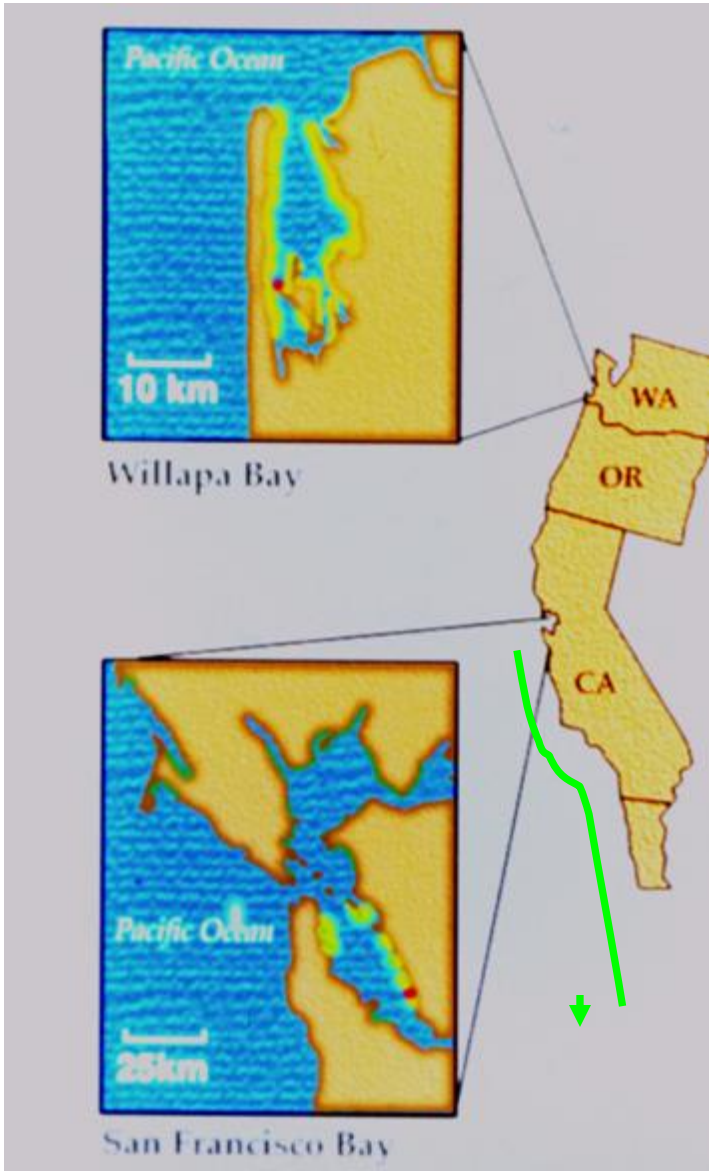
Hybrids *vs* Parental Species

- Higher variance in traits.
- **A few** transgressive genotypes have much higher fitness: vegetative growth, self fertility, pollen and seed production greater than either parental species.
  - Larger, denser, deeper roots, more rapid lateral expansion. Self fertile, grow higher and lower in the marsh.
  - Higher spread rate and shorter doubling time.

V. Control

Zhang, Y. H., et al. (2012). "Interactions between mangroves and exotic Spartina in an anthropogenically disturbed estuary in southern China." Ecology 93(3): 588-597.

A Tale Of Two Estuaries



Willapa Bay, WA, USA

a. *Spartina alterniflora* introduced 100 years ago.

b. No native *Spartina*, no hybridization.

c. Spread rate low and constant.

"Slow motion" invasion.

d. Allee effect, little self pollination.

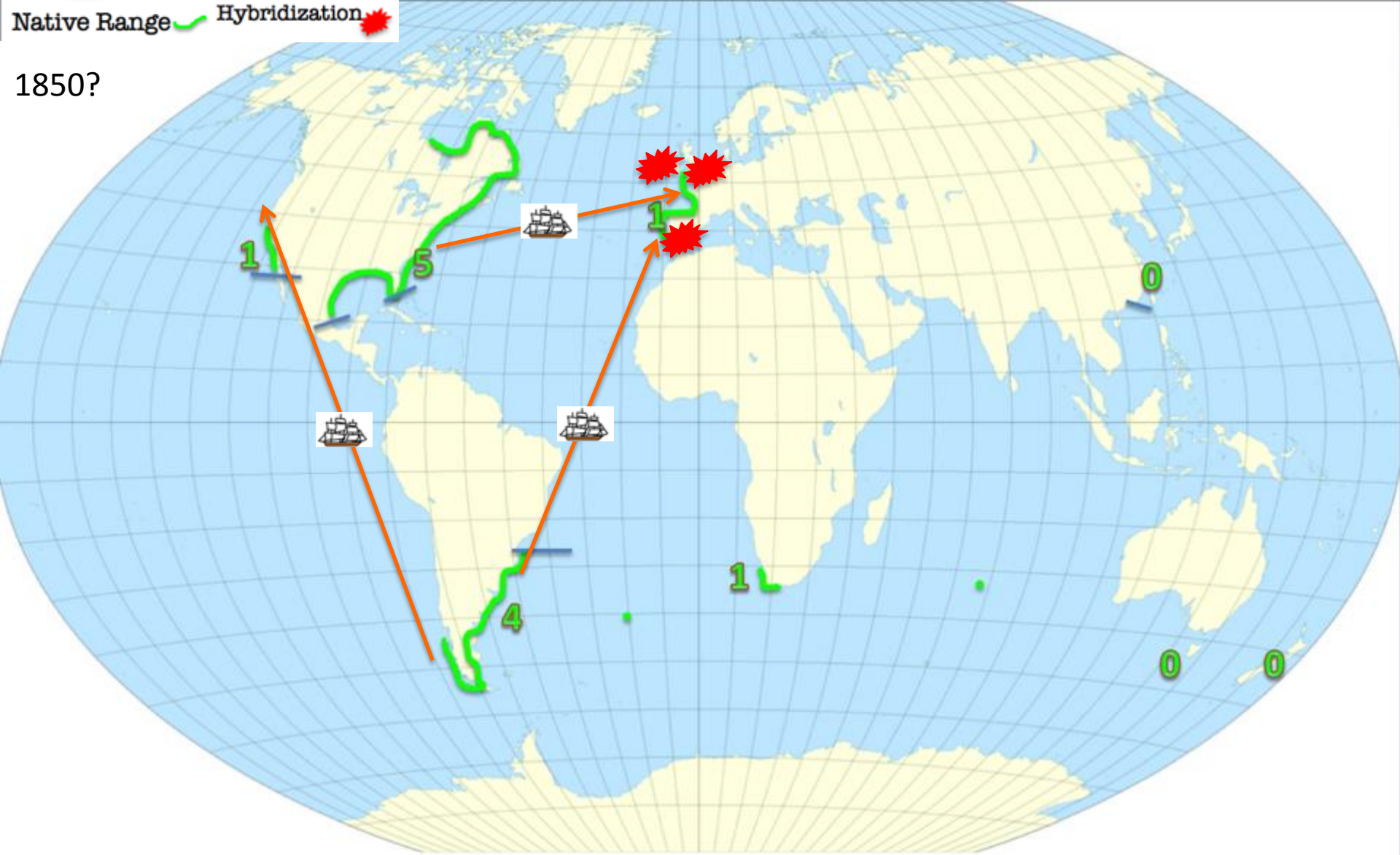
San Francisco Bay, CA,USA

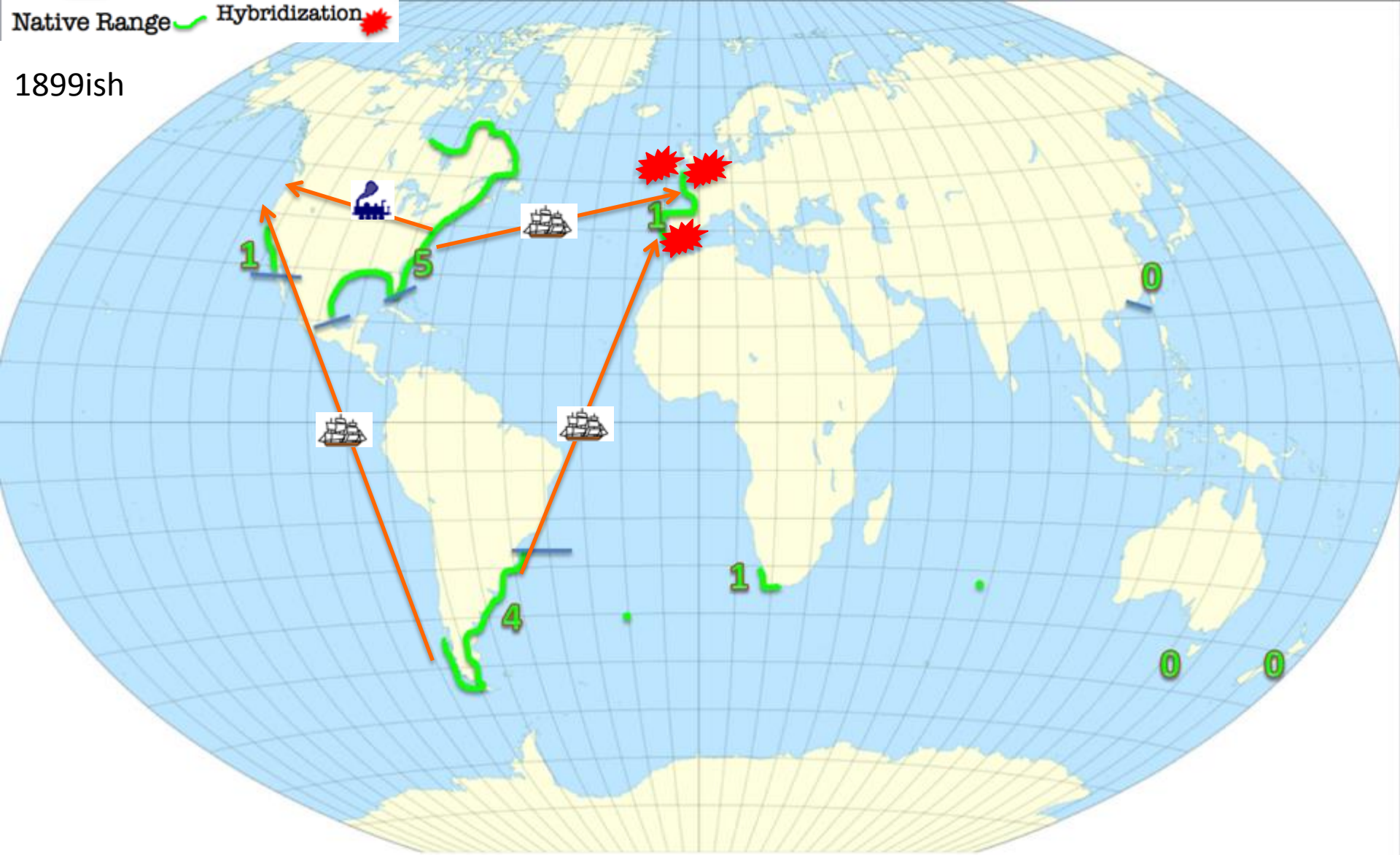
a. S*. alterniflora* x *S. foliosa*, 40 yrs ago.

b. Rapid spread. Extinction of *S. foliosa*?

d. Evolution of self fertility, no Allee effect.

Ayres, D. A & al. publications from 1999 – 2008.

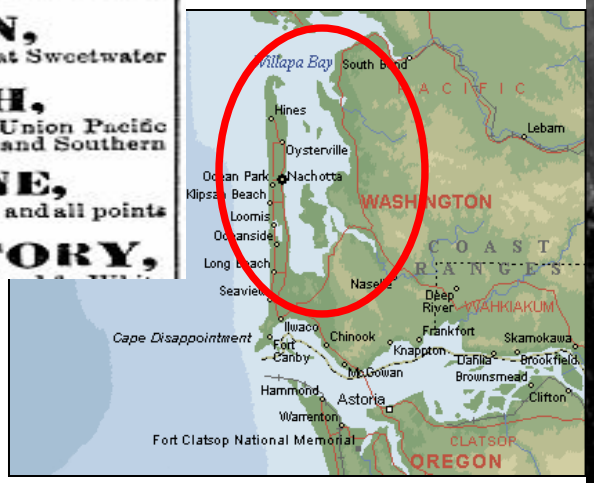

Native Range
Hybridization
1850?
1
5
1
0
1
4
0
0

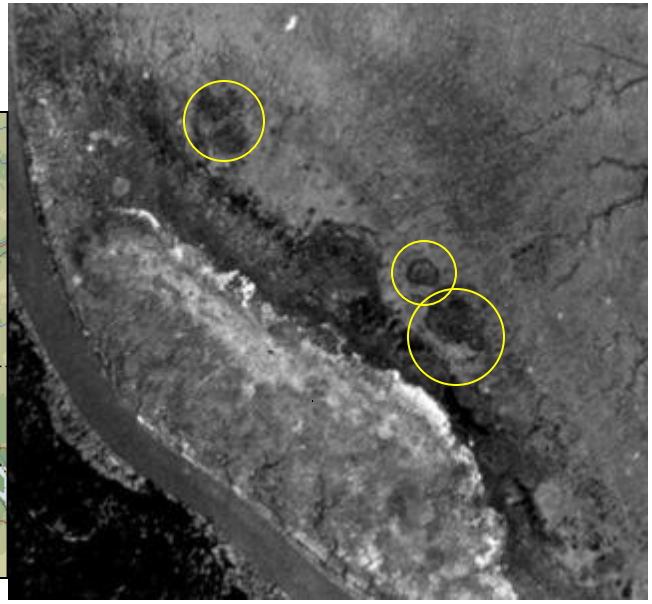

Native Range
Hybridization
1899ish
1
5
1
0
1
4
0
0

Willapa Bay WA. 1890's

Spartina alterniflora introduced by train, with live oysters from New York Harbor.


Train wreck on the pier near Bwaco, May 22, 1899.

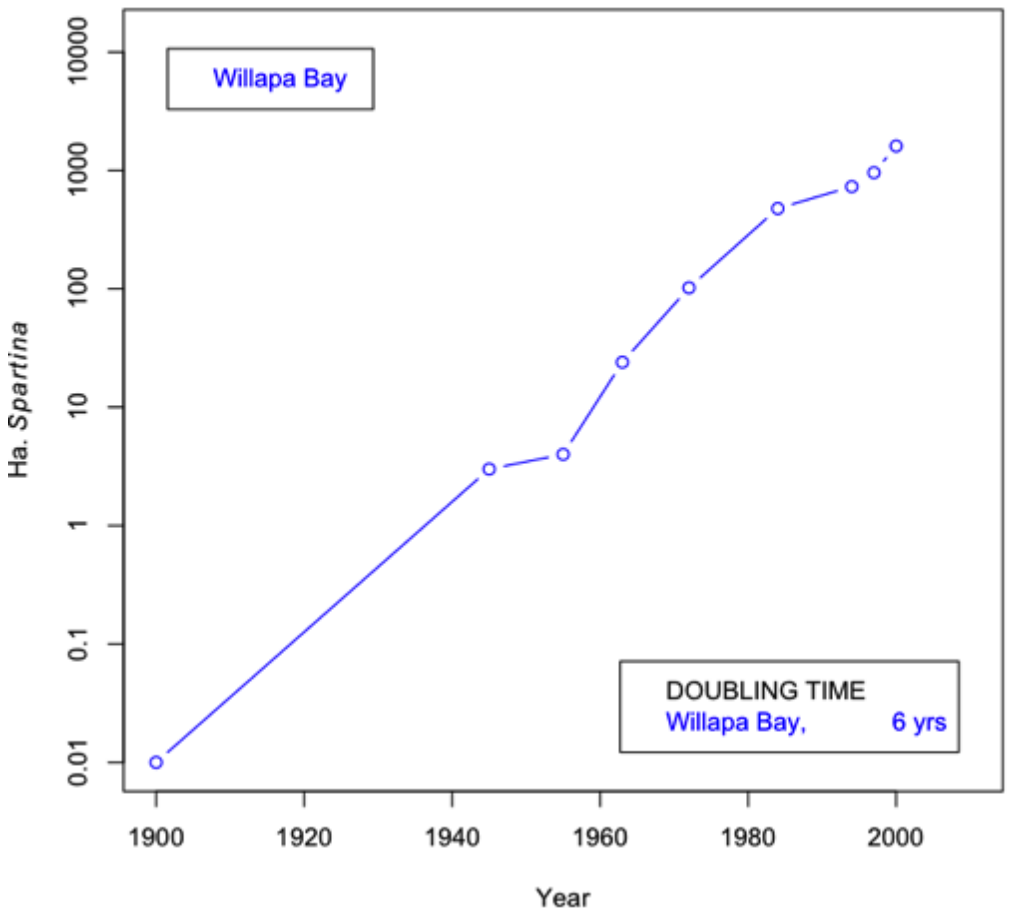




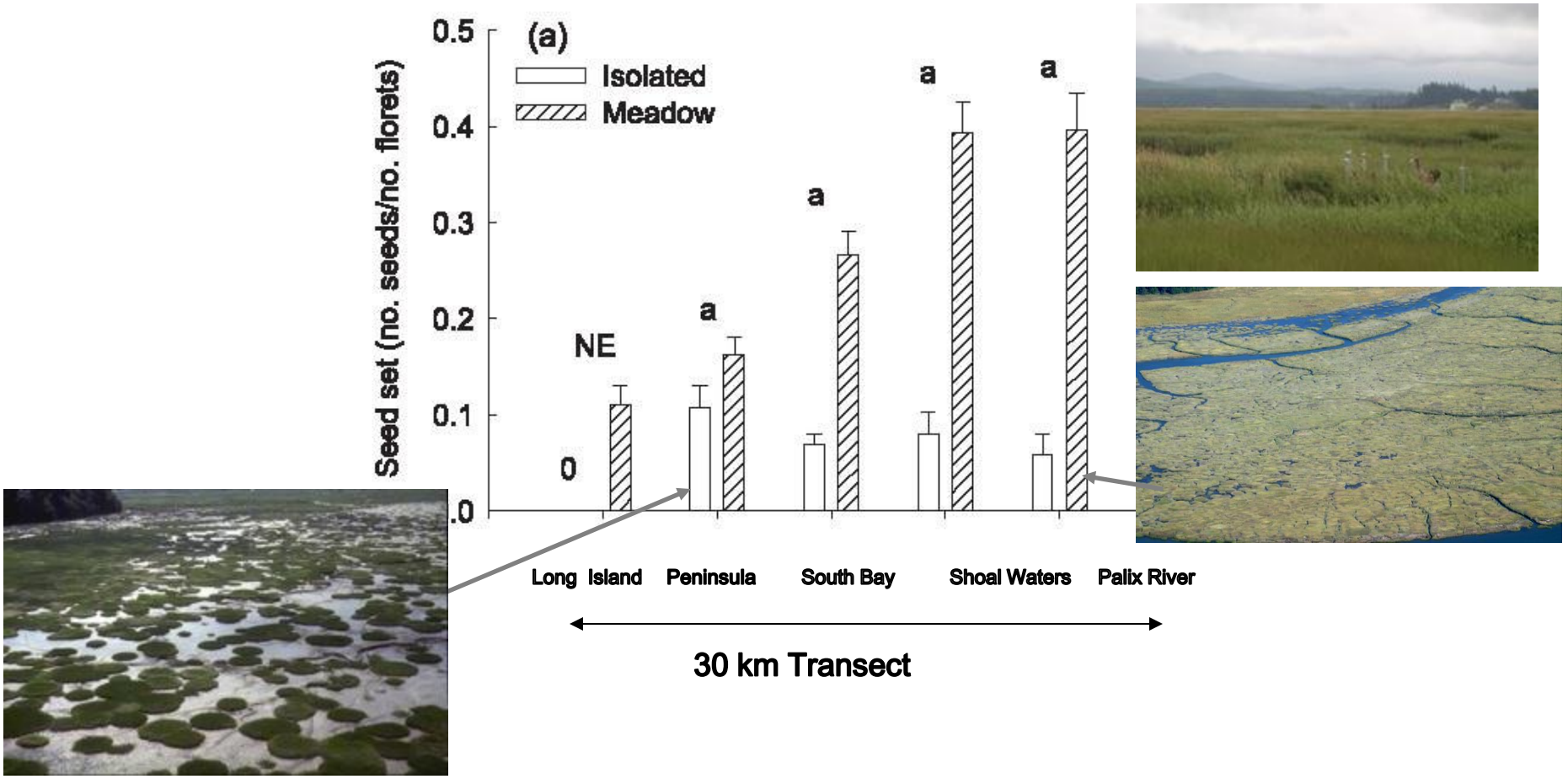
1942

Civille al. 2005. Reconstructing a century of Spartina alterniflora invasion with historical records and … remote sensing Ecoscience 12(3): 330.

Willapa. History. Graph



Young, isolated plants at leading edge of the invasion set little seed. Older, coalesced meadow plants set lots.



Davis & al. 2004. An Allee effect at the front of a plant invasion: Spartina in a Pacific estuary. J. Ecol. 92: 321.

for want of pollen

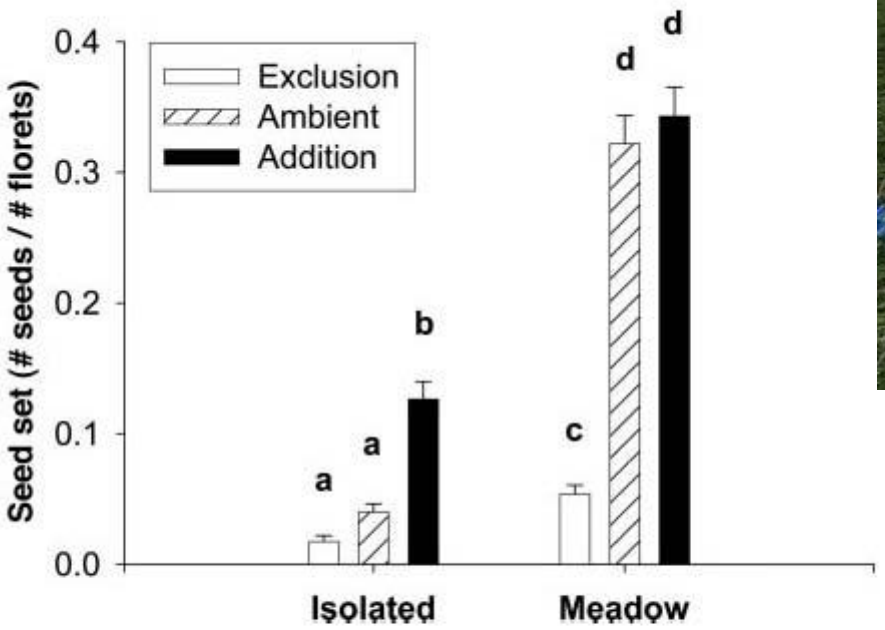


Fig. 3. Mean seed set (+1 SE) of pollen exclusion (open), ambient or open-pollinated (hatched), and pollen addition (black) treatments for isolated and meadow plants. Bars with different letters are statistically different at $P < 0.01$. All treatments were applied to 24 plants, and addition and ambient only to a further 20 plants.

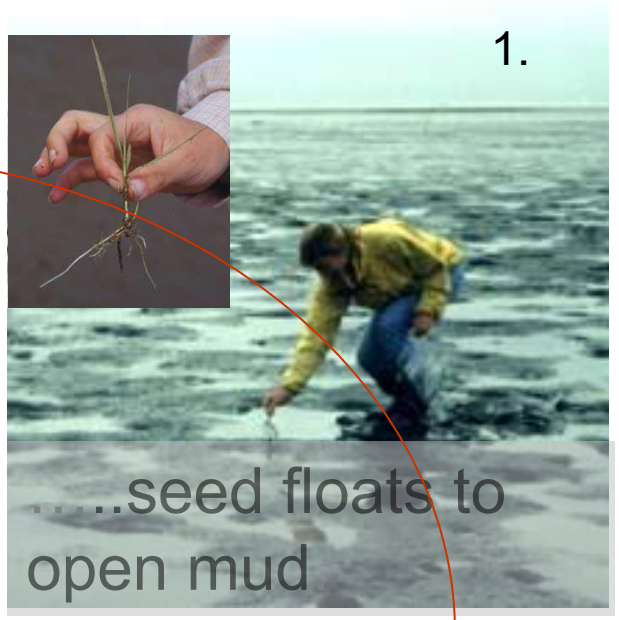
Davis & al 2004. Pollen limitation causes an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). PNAS 101:13804.

The lack of pollen
at the leading edge of the invasion
caused
low seed set
and
created a weak Allee Effect
in Willapa Bay.

This was an invasion in slow motion.

Invasion Cycle in Willapa Bay, WA

Only when clones coalesce into meadows, is pollen density sufficient for high seed set. 4.



1. …..seed floats to open mud

…for decades without producing much seed. 3.

2. Plants grow……

Hybrid *S. alterniflora x S. foliosa* in San Francisco Bay, since ≅ 1970

1. F1s are very rare.

   None found in field. In lab, 4/100s of crosses.

2. Introgressive backcrossing produced a hybrid swarm. Hybrid pollen overwhelms native stigmas, native moms produce hybrid seed.

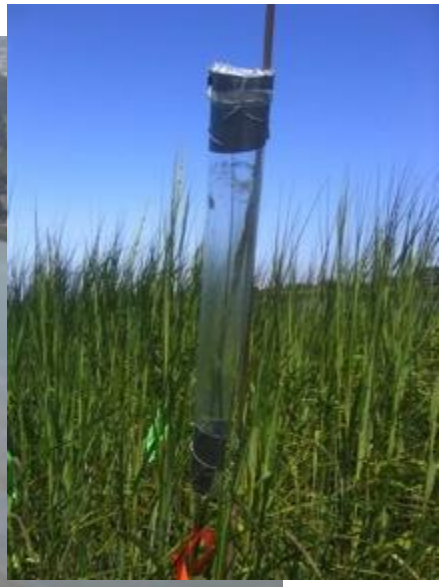
3. Bi-directional. Hybrid pollen to stigmas of both parental species (cpDNA).

4. A few hybrids are transgressive: fast growing, huge, and/or very fertile. ☞spread rapidly.

Evolution of Self Fertility …

Debra Ayres & Christina Sloop

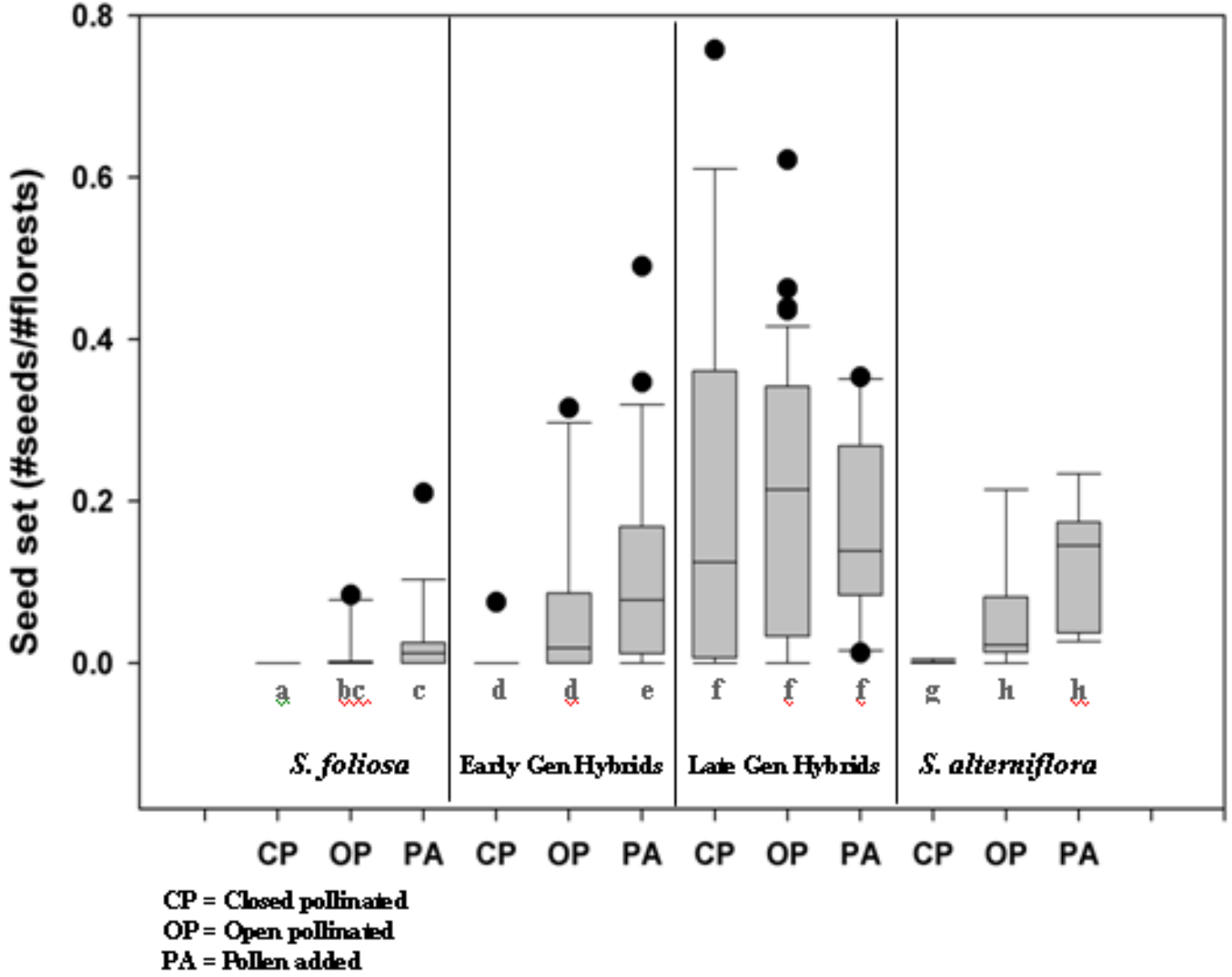
Evolution of Self Fertility



Early generation hybrids

Late Generation Hybrids

Sloop & al. 2010. Spatial and temporal genetic structure in a hybrid cordgrass invasion. *Heredity* 1-10.

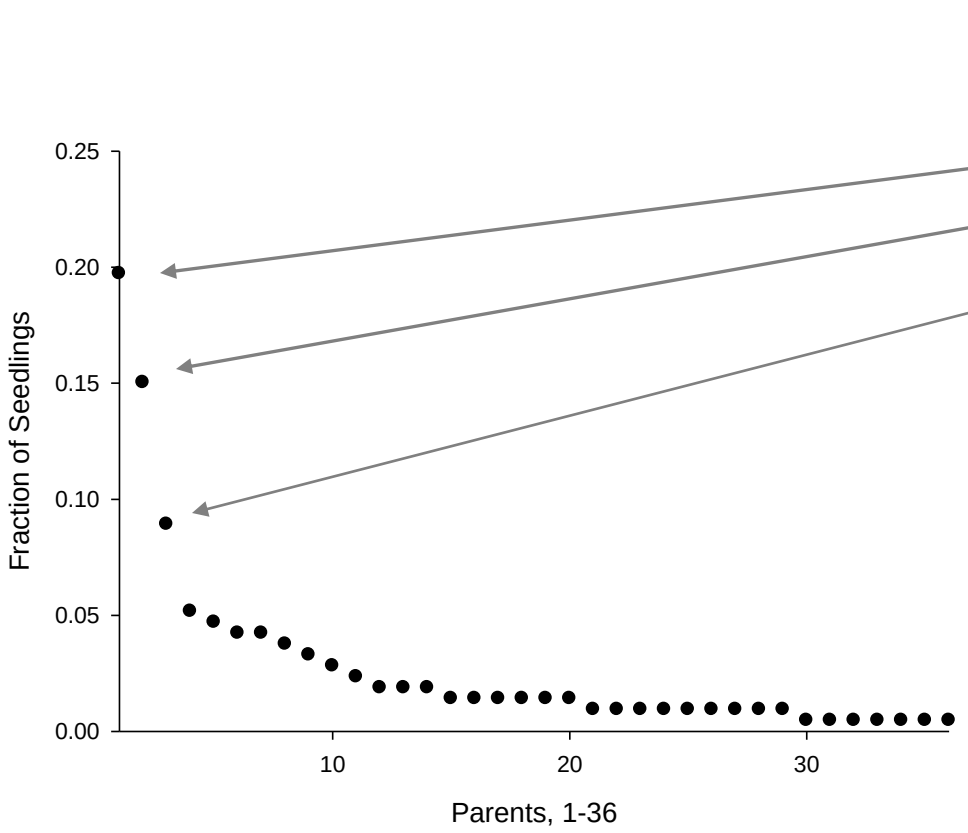


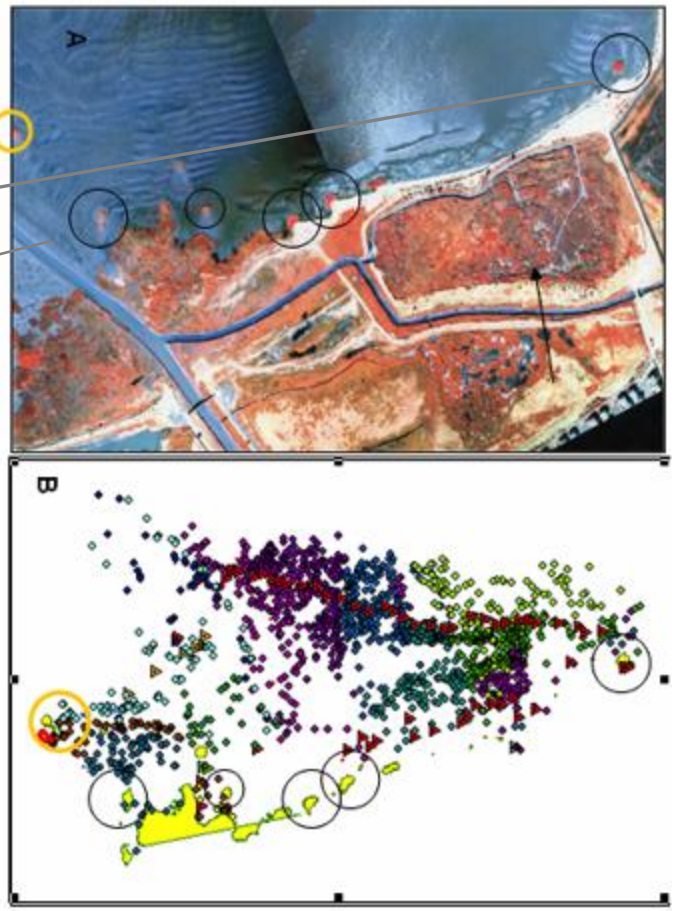
Sloop et al. 2009. The rapid evolution of self-fertility in Spartina hybrids (Spartina alterniflora x foliosa) invading San Francisco Bay, CA. Bio. Invas.11(5): 1131.

Some Late Generation Hybrids are Self Fertile & Set Much Seed.

Microsatellite Determination of Hybrid Parentage.

Moms (circles), Seedlings (diamonds), & Genotyped Seedlings (triangles)





3 self fertile moms were parents of 44% (of 213) of the genotyped seedlings.

67% of seedlings were the product of selfing.

The top three moms had the highest rates of selfing, by far.

Invasion Cycle in San Francisco Bay (Short Circuit!)

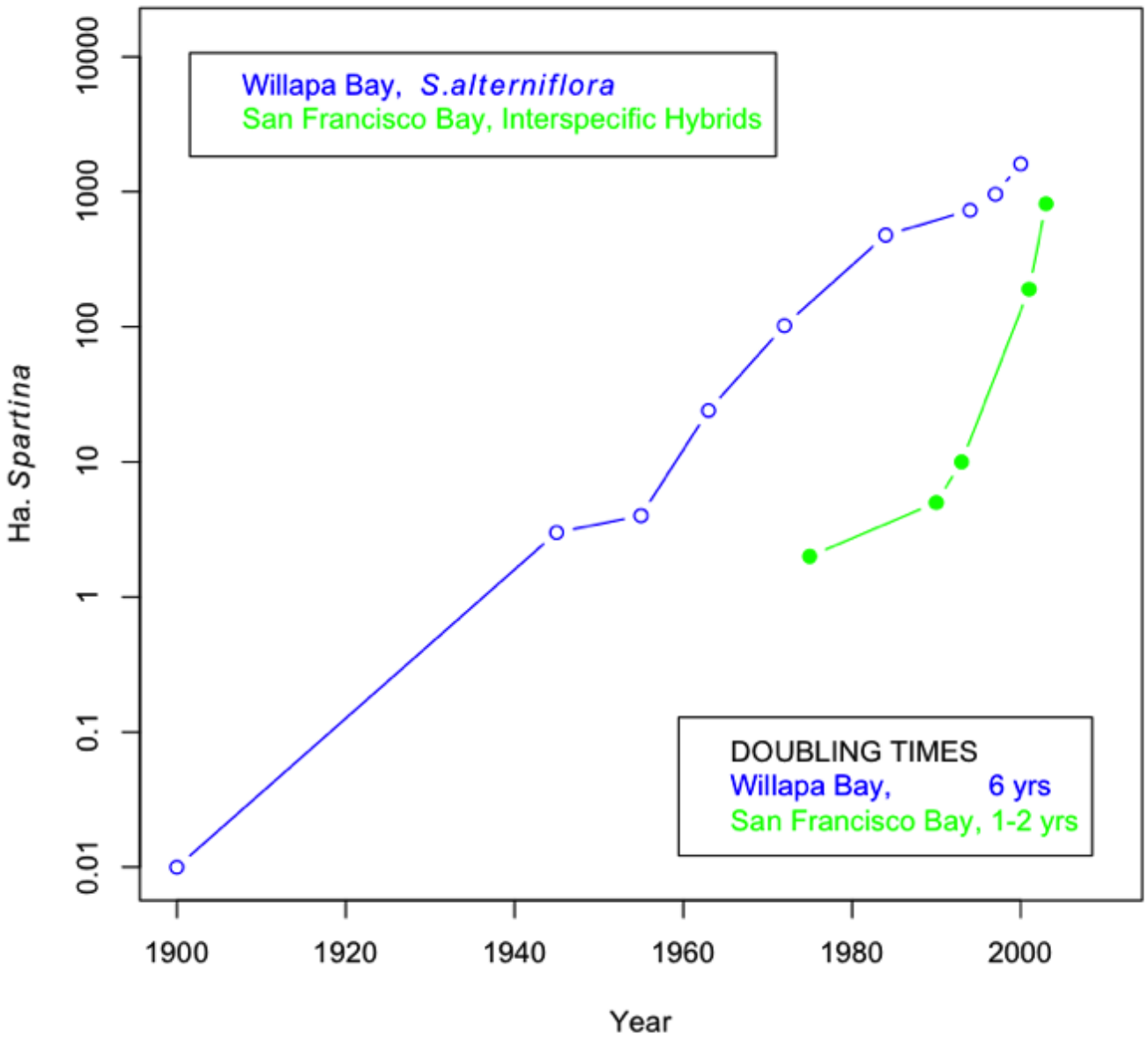
Cordgrass meadows now contain both early and later generation hybrids.

…..that colonizes open mud flats.

Self-compatible hybrids set seed

Backcross, and in a few generations….

Hybrid Plants grow,


Willapa Bay, S.alterniflora
San Francisco Bay, Interspecific Hybrids
DOUBLING TIMES
Willapa Bay, 6 yrs
San Francisco Bay, 1-2 yrs
Ha. Spartina
0.01
0.1
1
10
100
1000
10000
1900
1920
1940
1960
1980
2000
Year

Twisted Sisters: Polyploidy, Hybridization, and Reticulate Evolution in *Spartina* History.

1491➔

Time ➔

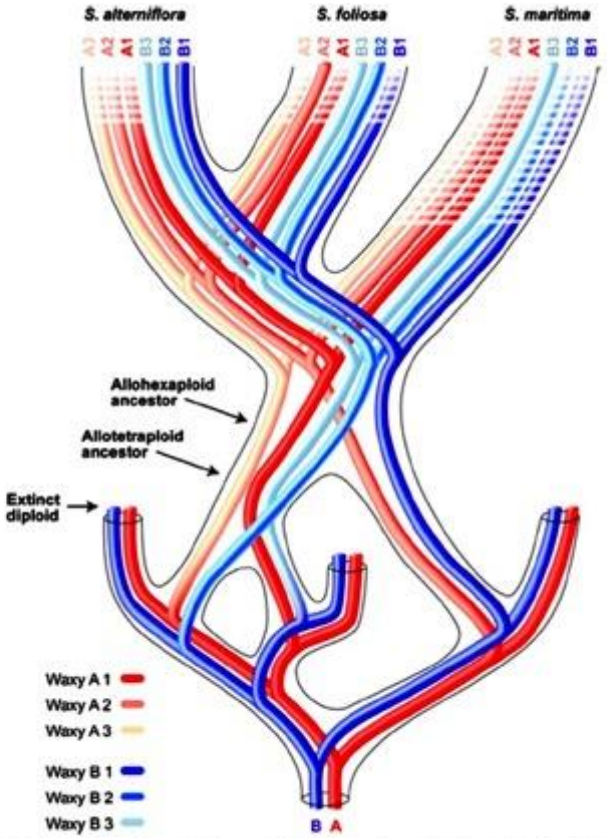


Fig. 5. Inheritance of two (A and B) paralogous *Waxy* copies in hexaploid *Spartina*, assuming a reticulate origin of the polyploids from three, now extinct diploid ancestors that carried A1B1, A2B2, and A3B3 copies, respectively. Dotted lines indicate lost or un-sampled copies in the present-day polyploids.

Fortune & al. 2008. The enigmatic invasive Spartina densiflora: A history of hybridizations in a polyploidy context. *Mol. Ecol.* **17**(19): 4304.

Spartina is a powerful ecological engineer, a trait that first brought **admirers**, then
uneasy allies,
and now **distrust** from those concerned with the environment.

As illustrated in *Spartina* introductions:

a. New Zealand,

b. Willapa Bay WA, USA,

c. San Francisco Bay CA, USA,

d. China.

The San Francisco Estuary.

70% of the mudflats in California.
> 350,000 migrating shorebirds in fall, >900,000 spring.
Second only to Alaska in shore birds, Pacific coast of NA.

Native *Spartina foliosa*

short, sparse, & used heavily by shorebirds.

Shorebirds

have difficulty landing in and using dense *Spartina*.
All dense *Spartina* in SF Bay is hybrid *S. foliosa* x S. *alterniflora*. Hybrid *Spartina* spread could greatly reduce foraging area.

Herbicide campaign

against hybrid *Spartina.* 2001-2010.
Successful for shore birds; complications.