

# Biogeography and Trophic Ecology of Maine's Island Red-backed Salamanders (*Plethodon cinereus*)

Nikko Shaidani



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Michael T. Kinnison  
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# Outline

- I. Introduction to island biogeography
  - a. classic island biogeography
  - b. Maine's coastal islands
  - c. formation of contemporary islands
  - d. the island salamander system



- II. Chapter I: Population Structure and Biogeographic Origins

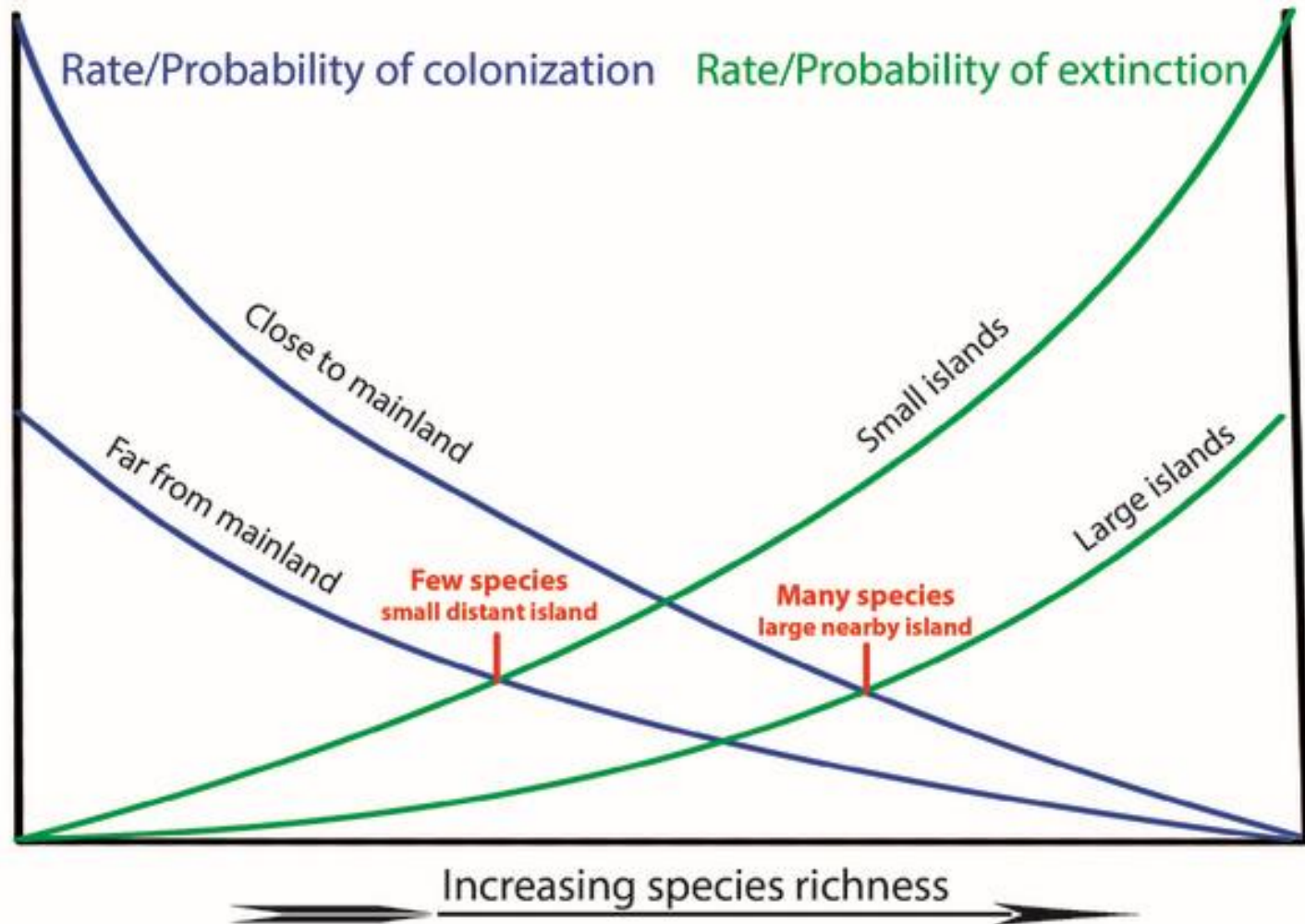
- III. Chapter II: Trophic Ecology and Morphological Variation

- IV. Summary of Results, Research Significance, and Management Implications



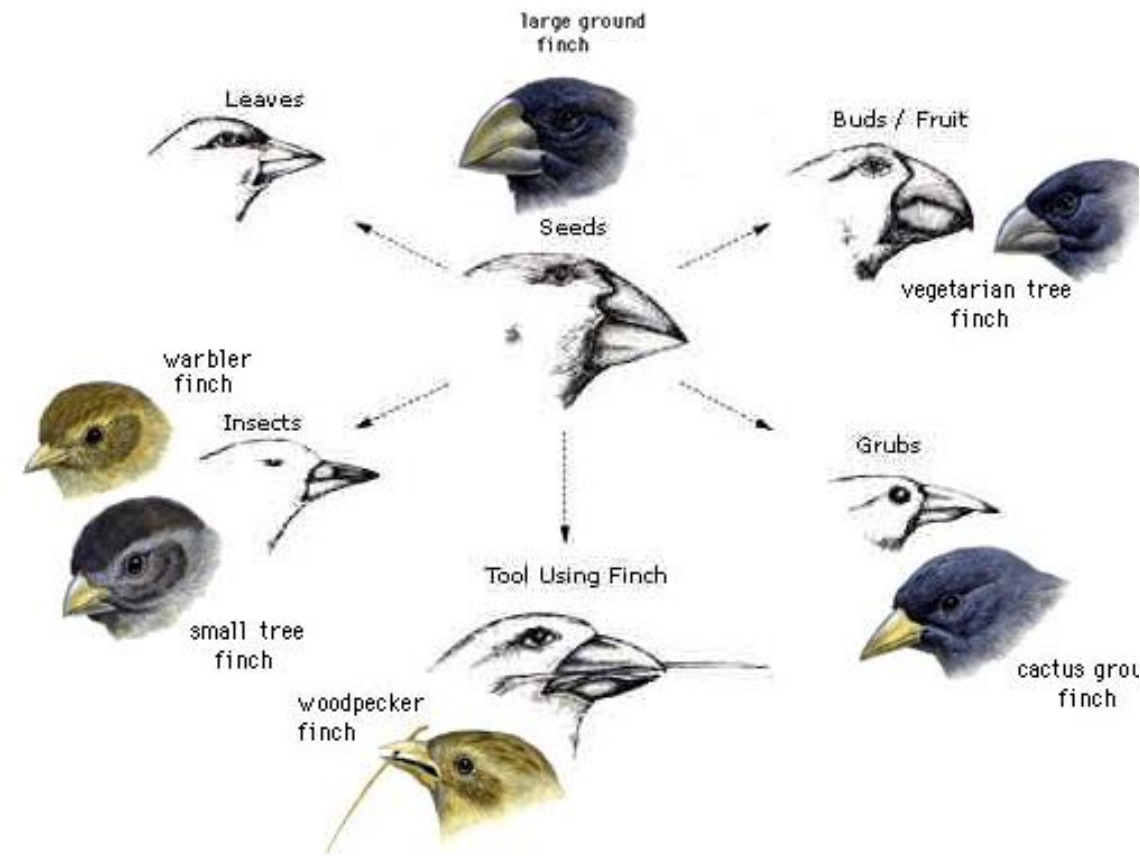
# Classic Island Biogeography

- Island colonization/extinction dynamics

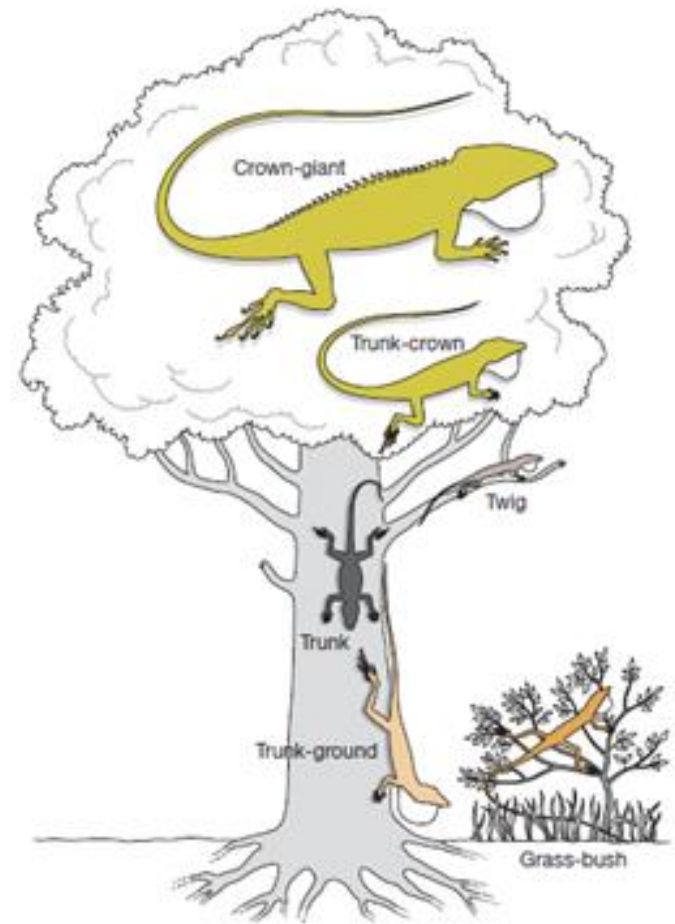


# Adaptive Radiation

vicariance, natural selection, and associated adaptive radiations



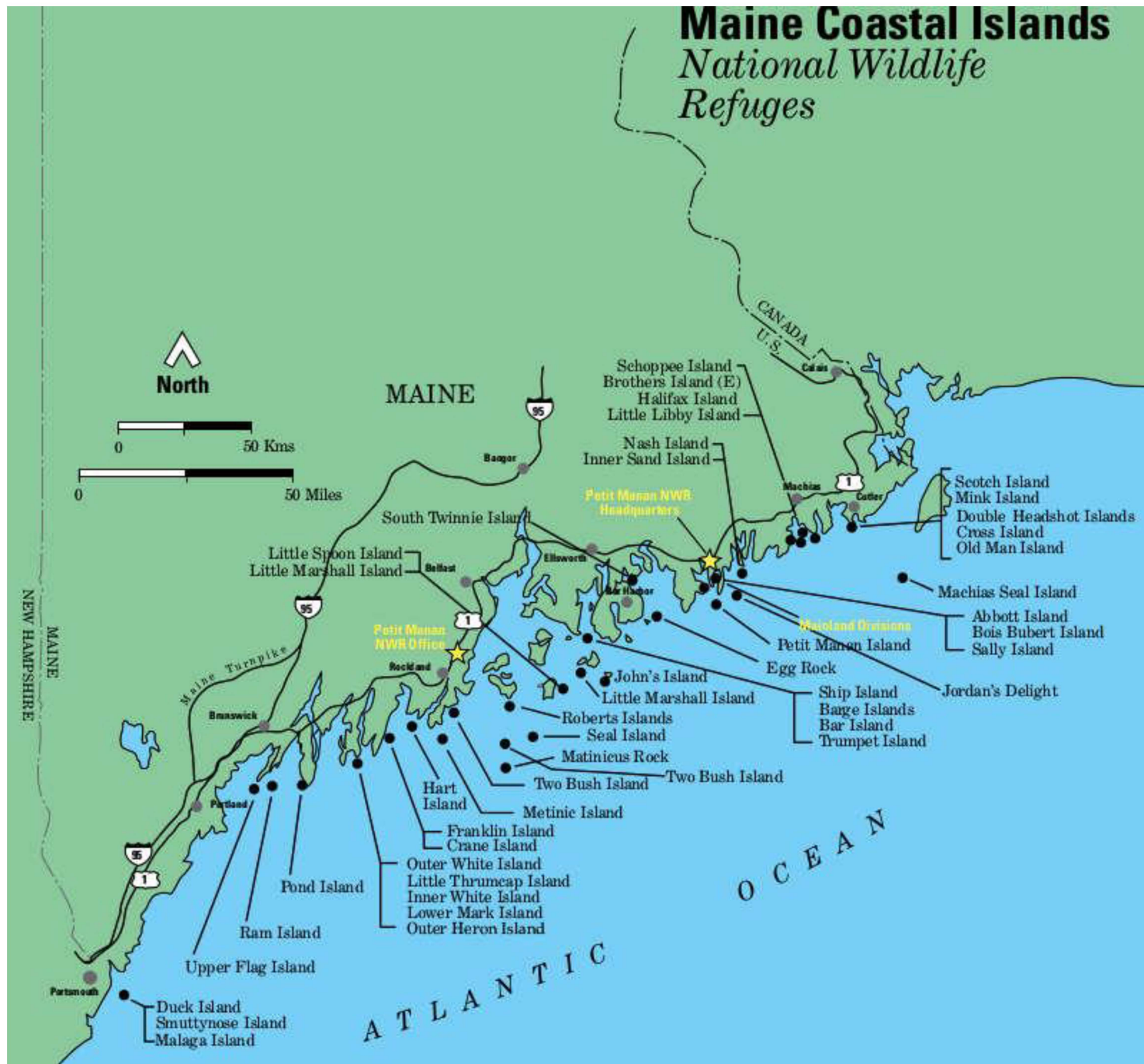
Boag and Grant 1981; Grant and Grant 1992



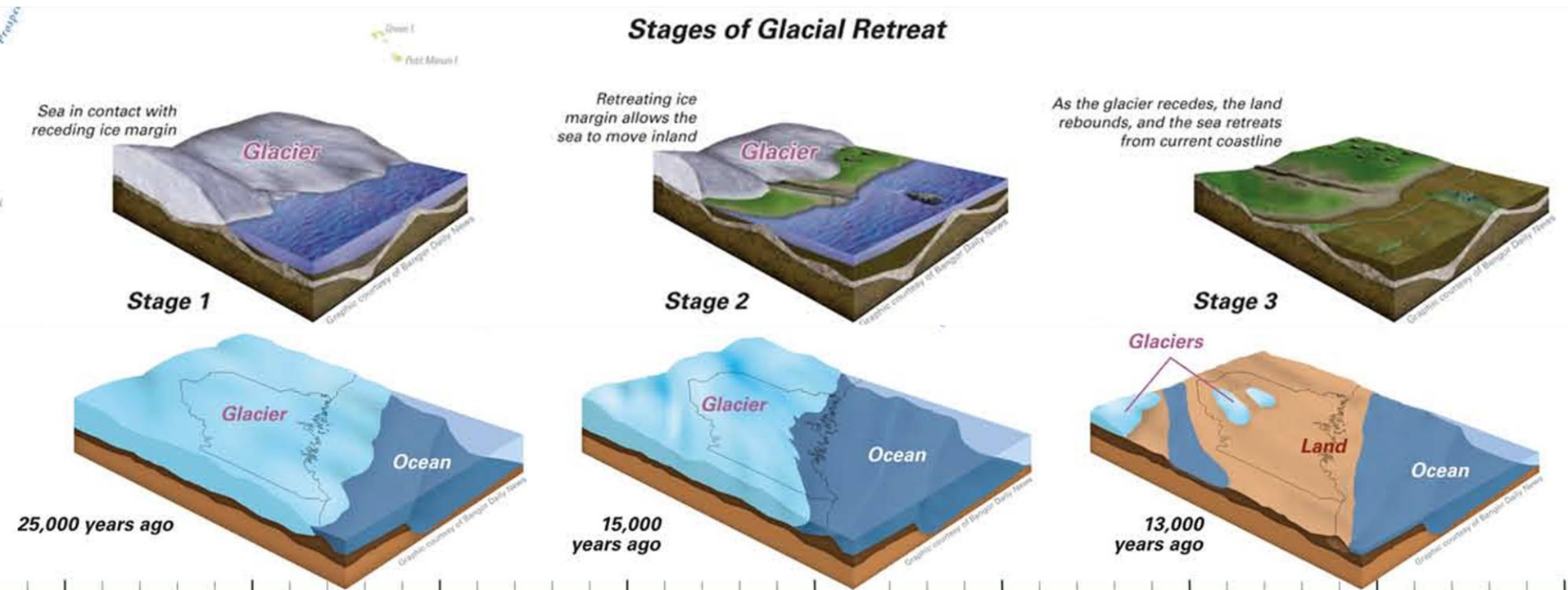
Losos 1990; Losos et al. 1997 and 1998

# Maine Coastal Islands

## National Wildlife Refuges



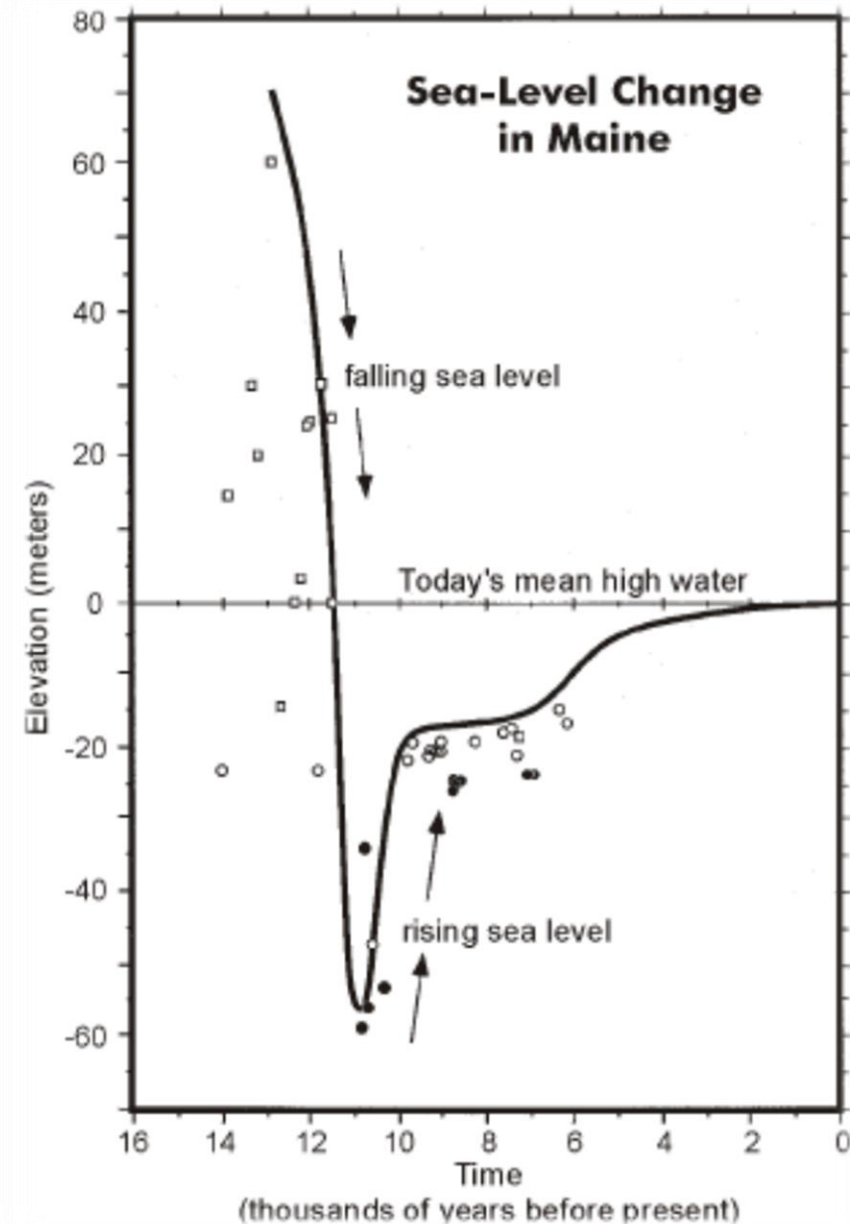
# Formation of contemporary islands



Ice Age Trail Map, University of Maine, 2006

# Formation of contemporary islands

- Sea Rise Over the Past 11,000 Years Has Resulted in the Isolation of Modern Day Islands



Barnhardt et al. 1995

# The island salamander system

*Plethodon cinereus*



- Earliest record of red-backed salamanders: Shurtleff, 1862; Treats island

# The island salamander system

- Plethodontidae
- No aquatic larval stage
- moist habitats of evergreen, mixed, and deciduous forest
- Found under logs, rocks, and leaf litter



# Reduced Dispersal

- Red-backed salamanders reduced dispersal behavior

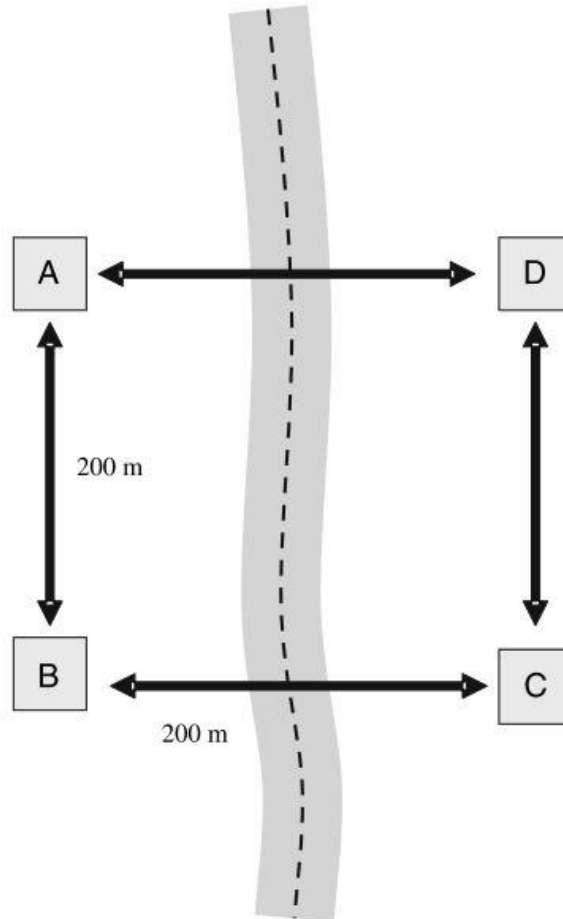


**Fig. 1** Sampling design for each of the road sites. Approximately 48 salamanders were collected from each of the plots A, B, C, and D

- Marsh et al. 2008

# Reduced Dispersal

## Divergence at modest geographic scales

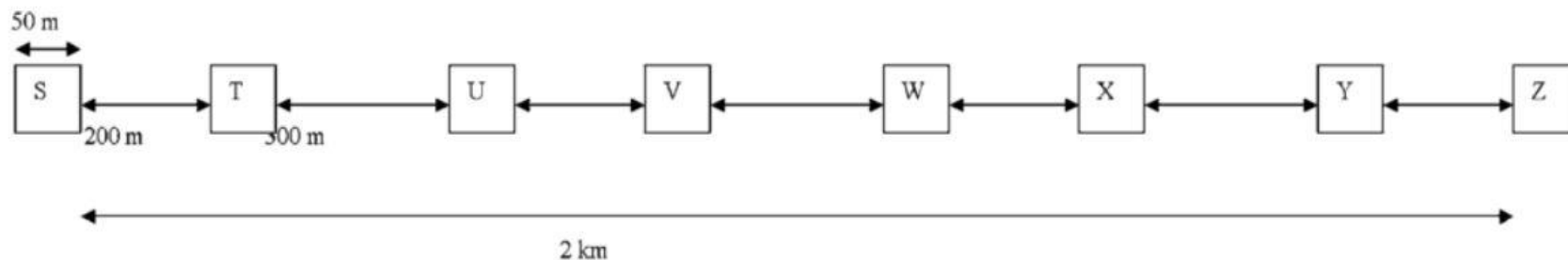


**Table 3** Pair-wise  $F_{ST}$  values and significance (above diagonal, \* < 0.05, \*\* < 0.005, \*\*\* < 0.0005) probability estimates based on 10 100 haplotype permutations

|   | S     | T     | U     | V      | W     | X     | Y     | Z   |
|---|-------|-------|-------|--------|-------|-------|-------|-----|
| S |       | **    | NS    | *      | **    | ***   | ***   | *** |
| T | 0.015 |       | ***   | ***    | ***   | ***   | ***   | *** |
| U | 0.002 | 0.029 |       | NS     | *     | *     | ***   | **  |
| V | 0.010 | 0.026 | 0.005 |        | NS    | NS    | ***   | *** |
| W | 0.013 | 0.035 | 0.008 | -0.003 |       | NS    | ***   | **  |
| X | 0.017 | 0.028 | 0.010 | 0.003  | 0     |       | ***   | *** |
| Y | 0.029 | 0.043 | 0.026 | 0.023  | 0.028 | 0.019 |       | *** |
| Z | 0.016 | 0.061 | 0.011 | 0.017  | 0.014 | 0.019 | 0.033 |     |

NS, nonsignificant.

# The island salamander system



- *P. cinereus* cannot survive extended salt water immersion
  - Islands vary in size and habitat
  - Island distance from mainland varies

# The island salamander system



- 1) Are island populations genetically isolated and divergent from one another and their mainland counterparts?
- 2) Are island populations subject to different ecological conditions that could drive adaptive divergence?

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# Chapter I: Population Structure and Biogeographic Origins



# Chapter I: Population Structure and Biogeographic Origins

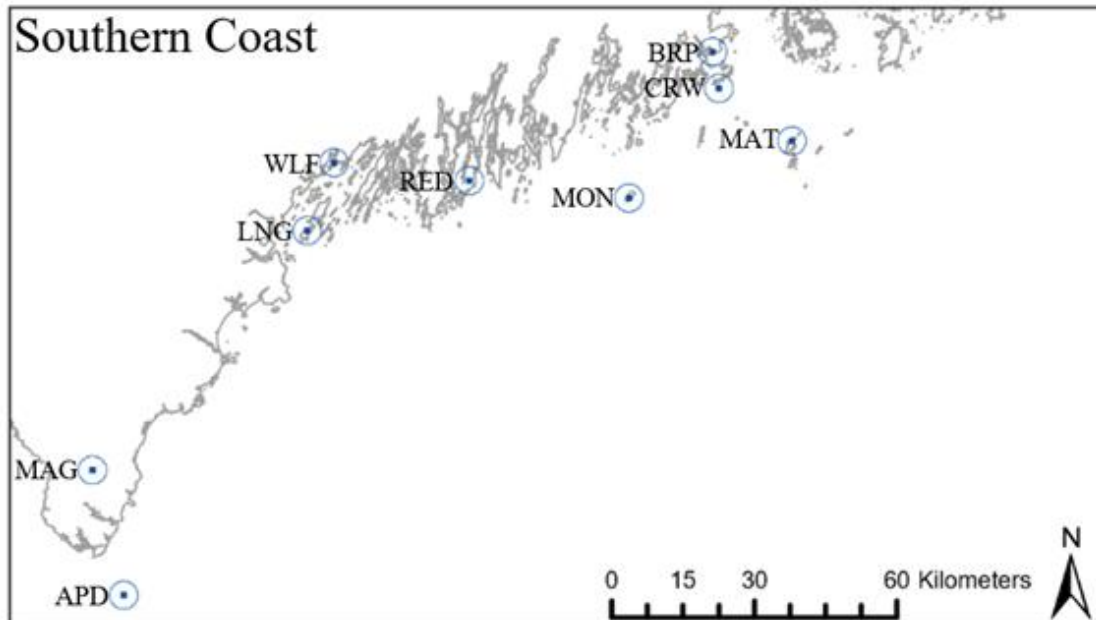
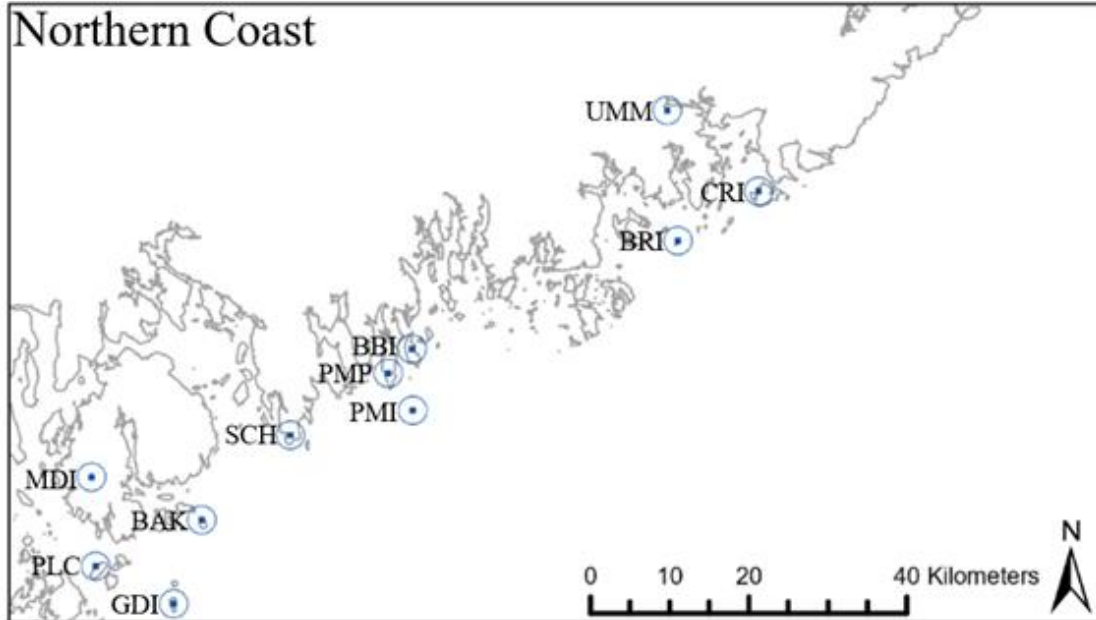
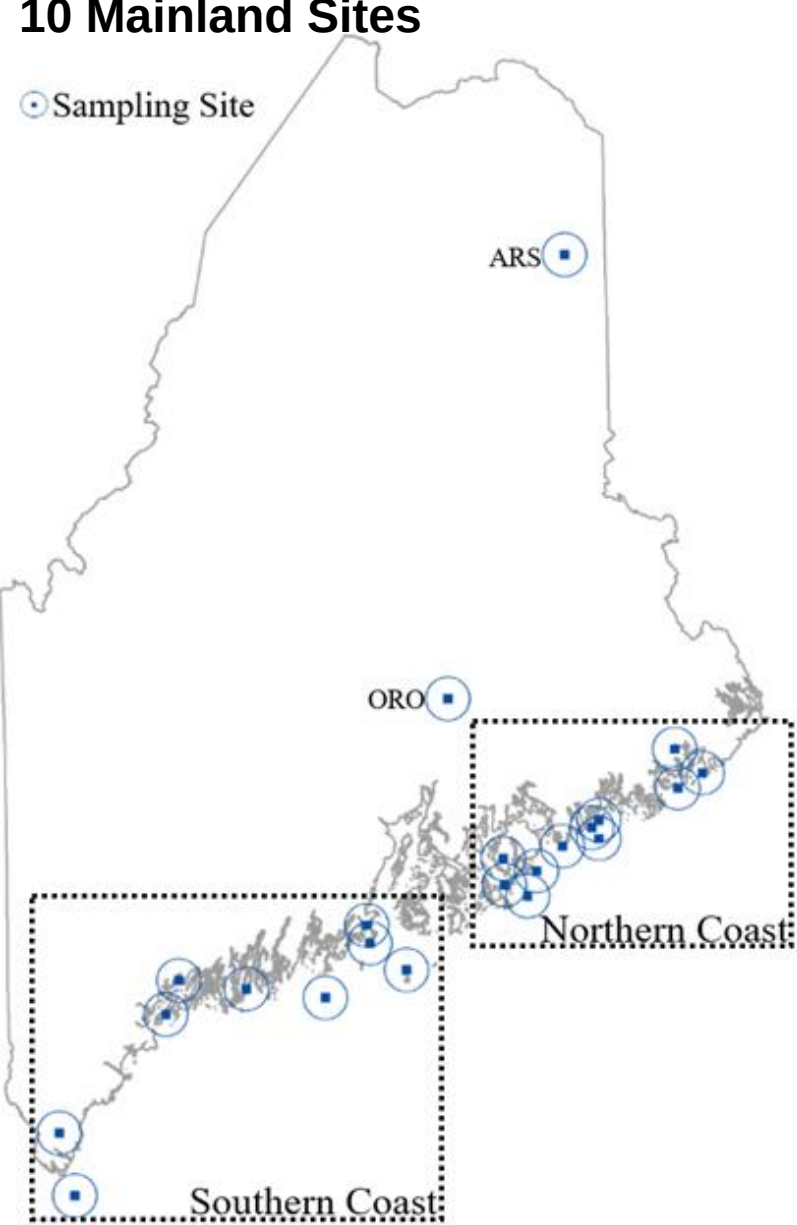


- How divergent are island populations from mainland populations and each other?
- How does genetic diversity on islands compare to mainland?
- How are island populations related to each other and mainland populations?

# Chapter I: Population Structure and Biogeographic Origins

12 Island Sites  
10 Mainland Sites

• Sampling Site



| Site                            | Site Type | Distance to Coast (km) | Dominant Vegetation |
|---------------------------------|-----------|------------------------|---------------------|
| Appledore Island                | I         | 10                     | Grass/Shrub         |
| Aroostook State Park            | M         | 200                    | Coniferous          |
| Baker Island                    | I         | 5                      | Coniferous          |
| Bois Bubert Island              | I         | 1                      | Coniferous          |
| Birch Point State Park          | M         | <0.5                   | Deciduous           |
| Cross Island                    | I         | 1                      | Coniferous          |
| Crow Island                     | I         | 5                      | Coniferous          |
| Great Duck Island               | I         | 10                     | Coniferous          |
| Isle au Haut                    | I         | 5                      | Coniferous          |
| Long Island                     | I         | 5                      | Coniferous          |
| Mount Agamenticus               | M         | 8                      | Deciduous           |
| Matinicus Island                | I         | 23                     | Coniferous          |
| Metinic Island                  | I         | 8                      | Coniferous          |
| Monhegan Island                 | I         | 17                     | Coniferous          |
| Mount Desert Island             | M         | 4                      | Deciduous           |
| Orono                           | M         | 50                     | Coniferous          |
| Outer Green Island              | I         | 8                      | Grass/ Shrub        |
| Placentia Island                | I         | 4                      | Coniferous          |
| Petit Manan Island              | I         | 4                      | Grass/ Shrub        |
| Petit Manan Point               | M         | 1                      | Grass/ Shrub        |
| Reid State Park                 | M         | <0.5                   | Coniferous          |
| Schoodic Education and Research | M         | <0.5                   | Coniferous          |
| Smuttynose Island               | I         | 10                     | Grass/ Shrub        |
| University of Maine at Machias  | M         | 5                      | Coniferous          |
| Western Brothers Island         | I         | 5                      | Grass/ Shrub        |
| Wolfe's Neck Woods State Park   | M         | <0.5                   | Coniferous          |

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# Chapter I: Population Structure and Biogeographic Origins

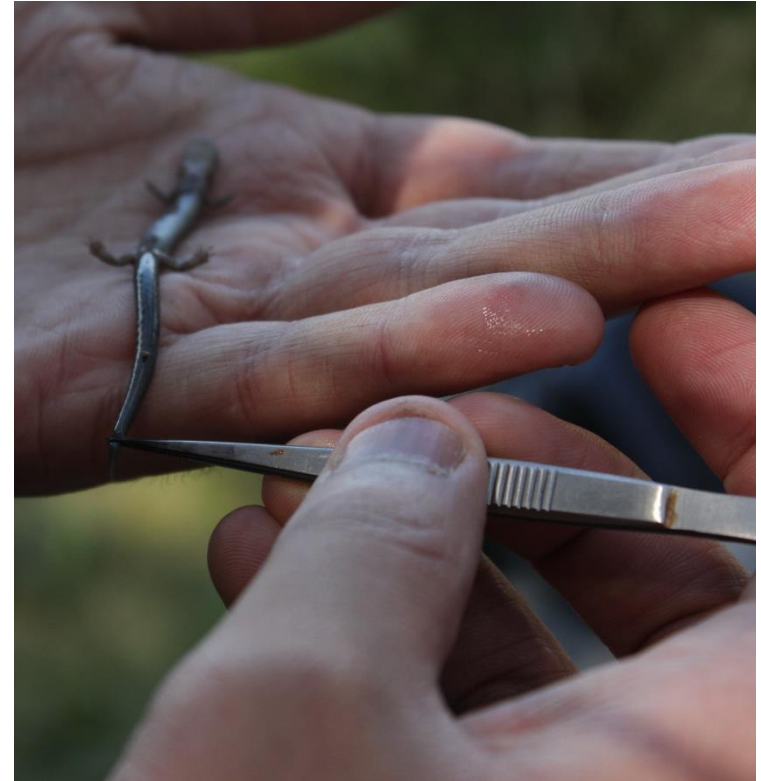
- Salamander capture



- Sedation via buffered MS-222 solution

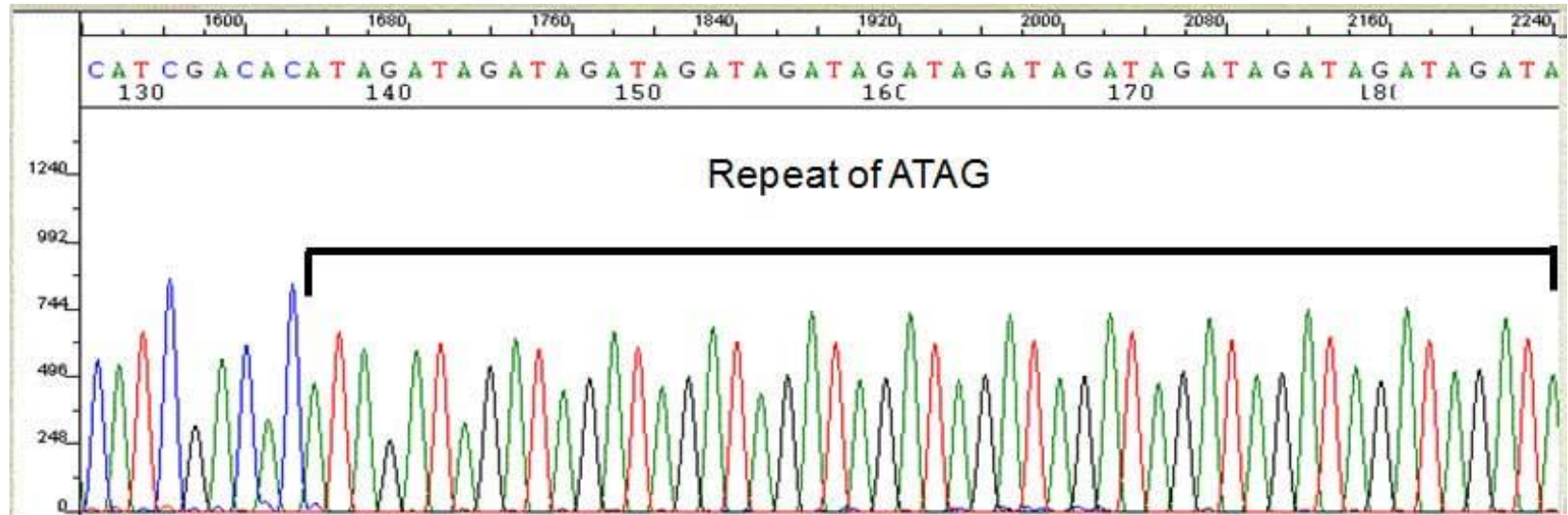
# Chapter I: Population Structure and Biogeographic Origins

- 3-5mm tail clips stored in 90% ethanol for genomic DNA extraction
- benzalkonium chloride antiseptic applied to the wound
- Forceps aseptitized by flame



# Chapter I: Population Structure and Biogeographic Origins

- we observed microsatellite DNA variation



- Short nucleotide sequences repeated
  - Tend to be highly polymorphic
  - Selectively neutral

# Chapter I: Population Structure and Biogeographic Origins

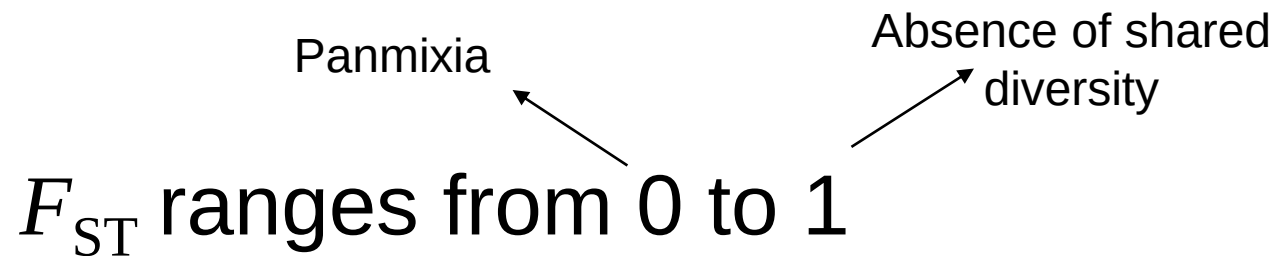
| Locus  | Primer sequence<br>with fluorescent tag or pigtail (5' → 3')       | Published source        |
|--------|--------------------------------------------------------------------|-------------------------|
| MS1718 | F: [PET]ATTCGGCATATTTTTCACTCTAA<br>R: GTTTGCAGCAGGTAGGTCTATCACG    | Fisher-Reid et al. 2013 |
| MS3241 | F: [VIC]GGTCCCCTTTGTATCTACTTTG<br>R: GTTTGCCGCCTAATTGCATTCC        | Fisher-Reid et al. 2013 |
| MS3544 | F: [6FAM]GCACAAAGCAAAGAGGAGAAA<br>R: GTTTCATTCATGTCTGAACTAGTGTG    | Fisher-Reid et al. 2013 |
| MS4953 | F: [PET]TGTGCGTCCTAAAAGCCATC<br>R: GTTTCACCTAGCTCACTTGCCC          | Fisher-Reid et al. 2013 |
| MS5155 | F: GTTTGCTTGAGGAGCTAAGTGATG<br>R: [6FAM]GCATGTGGCACGTAAAACAG       | Fisher-Reid et al. 2013 |
| MS6162 | F: [PET]GGTCTTTTTTGGAGCATGTTGA<br>R: GTTTGAGGA ACTCAAACCAGCAA      | Fisher-Reid et al. 2013 |
| PcJX06 | F: GTTTCCCTCCTAGAACCCAGAACC<br>R: [NED]TGGGTTAGGAAGGGAGAAATG       | Connors and Cabe 2003   |
| PcLX23 | F: [VIC]TTCTCTCAAAATGCATTAGACTGG<br>R: GTTTCCTAGTATGCCCCTTATCTGG   | Connors and Cabe 2003   |
| PcXF08 | F: GTTTAAGAACTCAGATTTTCCCTGTTTC<br>R: [NED]GGCAGGAATAACAAATGTACAAG | Connors and Cabe 2003   |

# Chapter I: Genetic Divergence

$F_{ST}$  = Fixation Index

$$F_{ST} = \frac{H_T - H_S}{H_T}$$

$F_{ST}$  ranges from 0 to 1



The diagram shows the text " $F_{ST}$  ranges from 0 to 1" at the bottom. Two arrows originate from this text: one points from the '0' to the word "Panmixia" located above and to the left, and the other points from the '1' to the phrase "Absence of shared diversity" located above and to the right.

Panmixia

Absence of shared diversity

# Chapter I: Genetic Divergence

$G'_{ST}$  = Standardized Measure for multiple loci

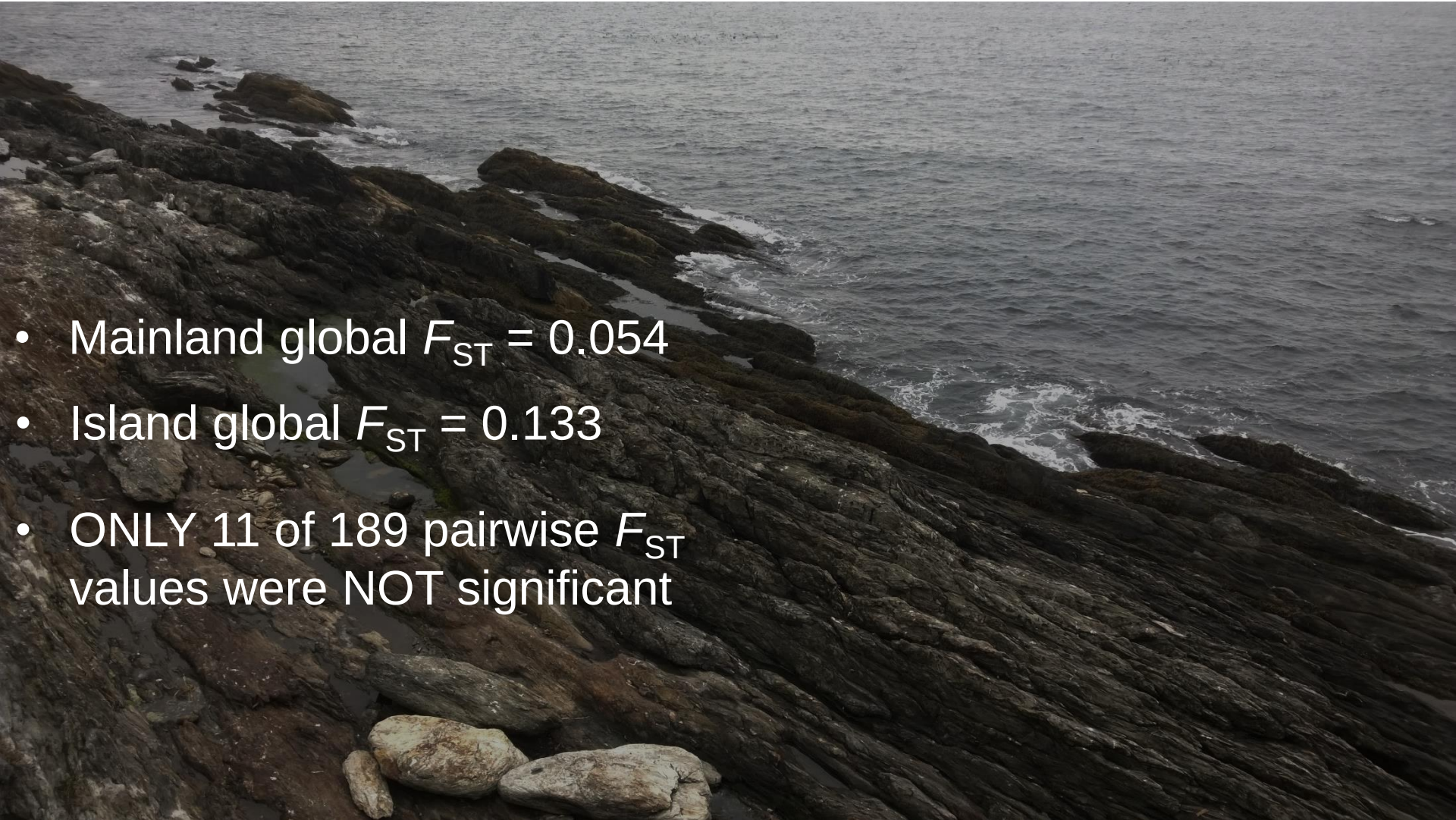
Calculated by dividing  $G_{ST}$  for a given marker by the maximum theoretical  $G_{ST}$  based on the heterozygosity at that marker

# Chapter I: Genetic Divergence

| Site | APD    | ARS     | BAK           | BBI            | BRP     | CRI            | GDI     | LNG     | MAG           | MAT     | MON     | MDI            | ORO     | PLC            | PMI     | PMP     | RED     | SCH     | UMM     | BRI     | WLF     |
|------|--------|---------|---------------|----------------|---------|----------------|---------|---------|---------------|---------|---------|----------------|---------|----------------|---------|---------|---------|---------|---------|---------|---------|
| APD  | ---    | 0.31111 | 0.24336       | 0.25838        | 0.26825 | 0.27542        | 0.5782  | 0.33079 | 0.37344       | 0.60294 | 0.43741 | 0.33478        | 0.33329 | 0.22972        | 0.30081 | 0.25953 | 0.31773 | 0.28916 | 0.29266 | 0.28165 | 0.24766 |
| ARS  | 0.1755 | ---     | 0.13363       | 0.15257        | 0.09011 | 0.15326        | 0.34524 | 0.17042 | 0.15138       | 0.56097 | 0.248   | 0.13295        | 0.16659 | 0.1815         | 0.25282 | 0.14307 | 0.12384 | 0.20409 | 0.15875 | 0.24809 | 0.1568  |
| BAK  | 0.1166 | 0.0803  | ---           | 0.02768        | 0.06175 | 0.03388        | 0.30946 | 0.07472 | 0.07063       | 0.5374  | 0.31974 | 0.00765        | 0.18695 | 0.04689        | 0.12629 | 0.09747 | 0.24846 | 0.08387 | 0.03043 | 0.14432 | 0.06955 |
| BBI  | 0.1112 | 0.0673  | 0.0085        | ---            | 0.02622 | -0.0234        | 0.26234 | 0.04816 | 0.03921       | 0.43705 | 0.28132 | -0.0087        | 0.15359 | 0.00858        | 0.08887 | 0.02312 | 0.16581 | 0.04315 | -0.0056 | 0.11033 | 0.06474 |
| BRP  | 0.1266 | 0.0499  | 0.0224        | <b>0.0077</b>  | ---     | 0.01778        | 0.26454 | 0.04368 | 0.05026       | 0.47307 | 0.24894 | 0.0378         | 0.18101 | 0.07807        | 0.1389  | 0.04793 | 0.07117 | 0.13011 | 0.03864 | 0.1381  | 0.0533  |
| CRI  | 0.1205 | 0.074   | 0.0126        | <b>-0.008</b>  | 0.0072  | ---            | 0.27257 | 0.03299 | 0.03512       | 0.47121 | 0.28217 | -0.0262        | 0.13321 | 0.00943        | 0.08744 | 0.05529 | 0.18337 | 0.06073 | -0.0184 | 0.09044 | 0.04719 |
| GDI  | 0.3038 | 0.1681  | 0.1278        | 0.1039         | 0.114   | 0.1093         | ---     | 0.28349 | 0.26498       | 0.4887  | 0.45571 | 0.28861        | 0.44358 | 0.30826        | 0.39785 | 0.31026 | 0.31245 | 0.32134 | 0.28112 | 0.41207 | 0.30922 |
| LNG  | 0.1614 | 0.0956  | 0.0304        | 0.0183         | 0.0185  | 0.0132         | 0.1165  | ---     | 0.03555       | 0.54862 | 0.31095 | 0.0338         | 0.15438 | 0.06212        | 0.12843 | 0.10749 | 0.16375 | 0.09848 | 0.06698 | 0.14635 | 0.02314 |
| MAG  | 0.1785 | 0.0726  | 0.0272        | 0.0151         | 0.0224  | 0.0154         | 0.1085  | 0.013   | ---           | 0.47014 | 0.29906 | 0.00576        | 0.09371 | 0.08951        | 0.17378 | 0.10653 | 0.16912 | 0.09402 | 0.06424 | 0.22869 | 0.06782 |
| MAT  | 0.3763 | 0.3022  | 0.2625        | 0.2115         | 0.2464  | 0.2358         | 0.2847  | 0.2718  | 0.2299        | ---     | 0.67455 | 0.51166        | 0.4803  | 0.47486        | 0.57534 | 0.37975 | 0.47883 | 0.43695 | 0.46857 | 0.62728 | 0.57979 |
| MON  | 0.2396 | 0.1121  | 0.1423        | 0.1158         | 0.1139  | 0.1196         | 0.2306  | 0.1413  | 0.131         | 0.3905  | ---     | 0.29963        | 0.38321 | 0.32968        | 0.29891 | 0.28844 | 0.21991 | 0.30236 | 0.32199 | 0.34522 | 0.27791 |
| MDI  | 0.1537 | 0.0653  | <b>0.0027</b> | <b>-0.004</b>  | 0.0121  | <b>-0.0075</b> | 0.1153  | 0.0138  | <b>0.0033</b> | 0.2573  | 0.1287  | ---            | 0.1092  | 0.0545         | 0.1011  | 0.07976 | 0.21963 | 0.07957 | 0.00314 | 0.1448  | 0.06309 |
| ORO  | 0.1963 | 0.0748  | 0.0728        | 0.054          | 0.0723  | 0.0501         | 0.1919  | 0.059   | 0.0397        | 0.2694  | 0.1798  | 0.0355         | ---     | 0.1286         | 0.25828 | 0.19096 | 0.27715 | 0.15658 | 0.15791 | 0.30704 | 0.14851 |
| PLC  | 0.1063 | 0.0905  | 0.0174        | <b>0.0034</b>  | 0.0313  | 0.0041         | 0.1376  | 0.0257  | 0.0341        | 0.2551  | 0.147   | 0.0193         | 0.0544  | ---            | 0.12921 | 0.06721 | 0.22479 | 0.0662  | -0.0062 | 0.10775 | 0.06302 |
| PMI  | 0.1352 | 0.1122  | 0.0424        | 0.0255         | 0.0504  | 0.0276         | 0.1647  | 0.0426  | 0.0589        | 0.2803  | 0.1324  | 0.0314         | 0.095   | 0.0444         | ---     | 0.09859 | 0.2202  | 0.14944 | 0.11279 | 0.11387 | 0.15492 |
| PMP  | 0.1271 | 0.0696  | 0.0354        | 0.0109         | 0.0228  | 0.0238         | 0.1352  | 0.0449  | 0.0427        | 0.2058  | 0.1423  | 0.0298         | 0.0797  | 0.0301         | 0.0331  | ---     | 0.13443 | 0.11454 | 0.07606 | 0.13605 | 0.13744 |
| RED  | 0.1647 | 0.0626  | 0.1071        | 0.0724         | 0.0331  | 0.0779         | 0.1471  | 0.0754  | 0.0852        | 0.2681  | 0.0991  | 0.0953         | 0.1398  | 0.1025         | 0.096   | 0.0705  | ---     | 0.23477 | 0.20557 | 0.24168 | 0.17288 |
| SCH  | 0.1394 | 0.0926  | 0.0317        | 0.0148         | 0.0464  | 0.0202         | 0.1379  | 0.0366  | 0.0318        | 0.2509  | 0.1433  | 0.0274         | 0.061   | 0.0248         | 0.0497  | 0.0472  | 0.1031  | ---     | 0.08401 | 0.22899 | 0.16129 |
| UMM  | 0.1337 | 0.0786  | 0.0099        | <b>-0.0037</b> | 0.0133  | <b>-0.0065</b> | 0.1202  | 0.0249  | 0.0249        | 0.2428  | 0.1406  | <b>-0.0016</b> | 0.0593  | <b>-0.0009</b> | 0.0356  | 0.0281  | 0.0947  | 0.0324  | ---     | 0.07855 | 0.06453 |
| BRI  | 0.1258 | 0.1215  | 0.0542        | 0.0405         | 0.0615  | 0.0355         | 0.1898  | 0.0615  | 0.0961        | 0.3319  | 0.1555  | 0.0549         | 0.1285  | 0.0421         | 0.0417  | 0.0592  | 0.1217  | 0.0872  | 0.0338  | ---     | 0.16776 |
| WLF  | 0.1357 | 0.0908  | 0.0274        | 0.0225         | 0.0204  | 0.0154         | 0.1246  | 0.0076  | 0.0295        | 0.288   | 0.1277  | 0.0211         | 0.0666  | 0.0241         | 0.0551  | 0.059   | 0.0778  | 0.0614  | 0.0219  | 0.065   | ---     |

- ONLY 11 of 189 pairwise  $F_{ST}$  values were NOT significant

# Chapter I: Genetic Divergence



- Mainland global  $F_{ST} = 0.054$
- Island global  $F_{ST} = 0.133$
- ONLY 11 of 189 pairwise  $F_{ST}$  values were NOT significant

# Chapter I: Genetic Divergence

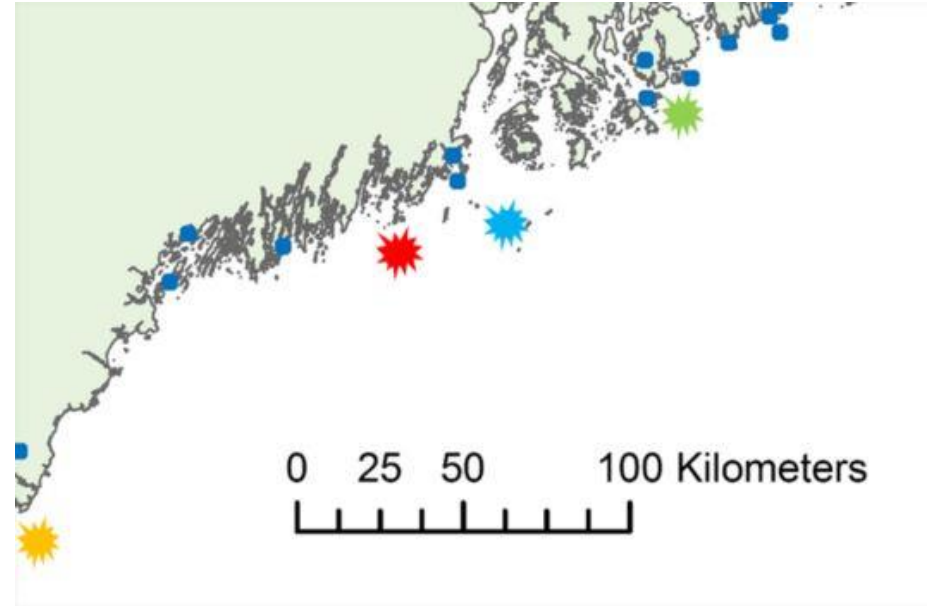
mean  $G'_{ST}$ :

Appledore Island =  $0.33 \pm 0.099$

Great Duck Island =  $0.35 \pm 0.086$

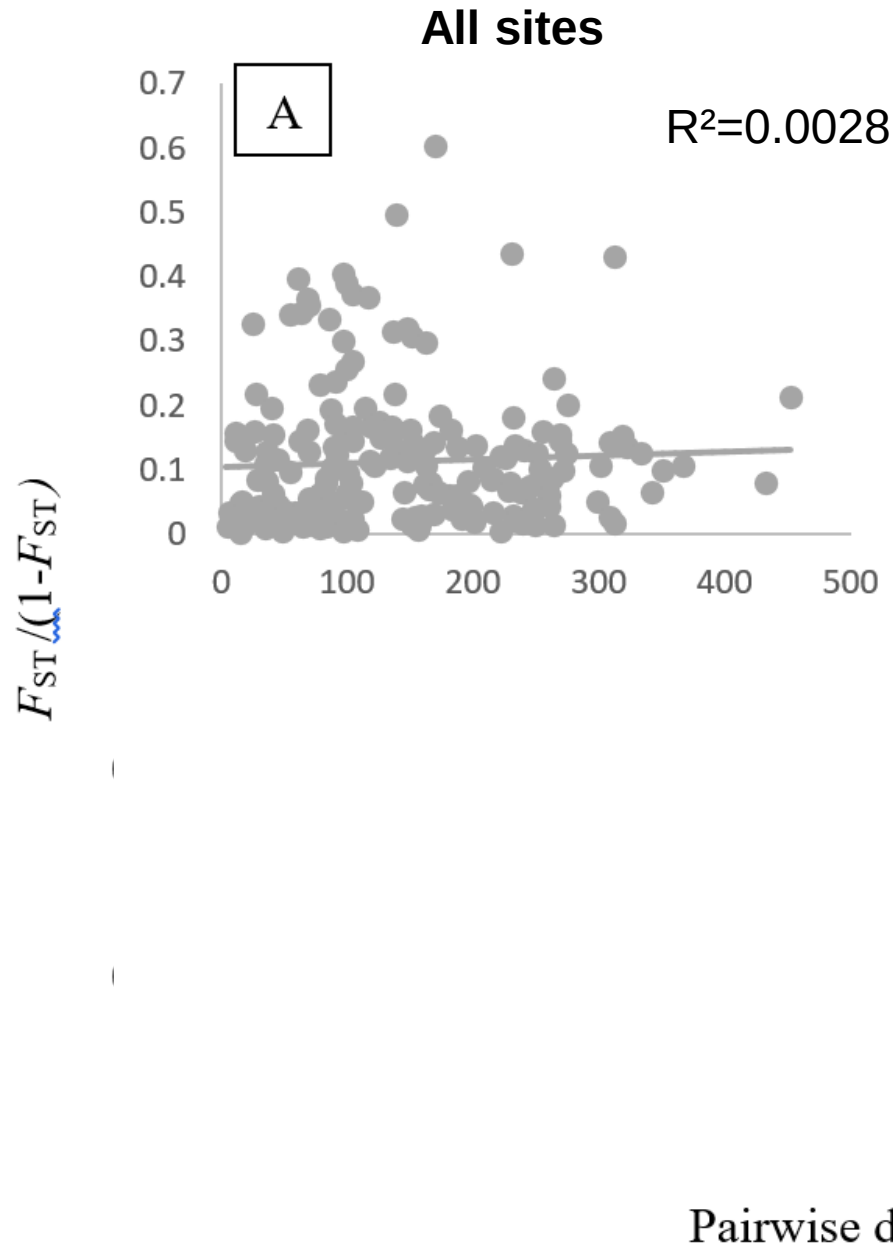
Matinicus Island =  $0.51 \pm 0.07$

Monhegan Island =  $0.33 \pm 0.097$



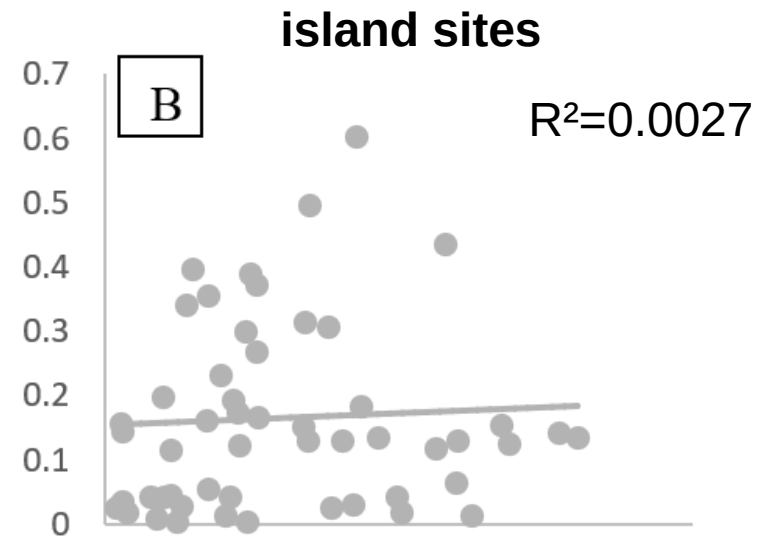
All others (excluding distant islands) =  $0.12 \pm 0.07$

# Chapter I: Genetic Divergence



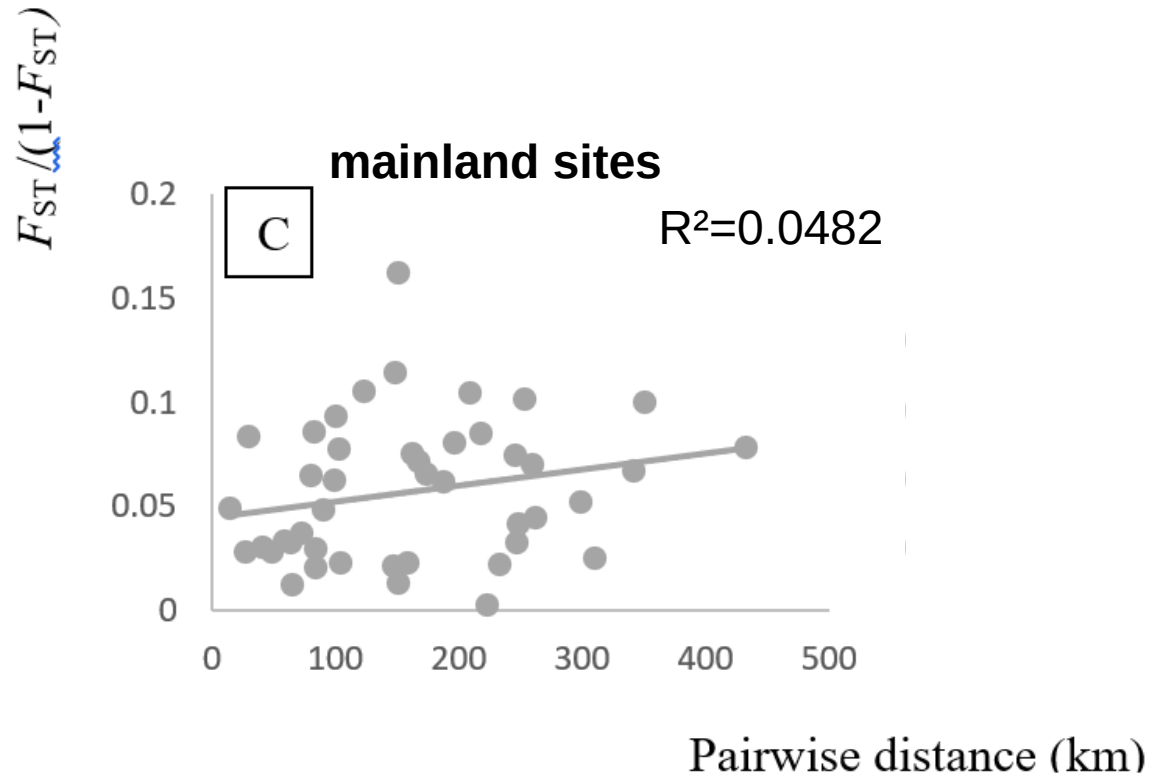
# Chapter I: Genetic Divergence

$F_{ST} / (1 - F_{ST})$



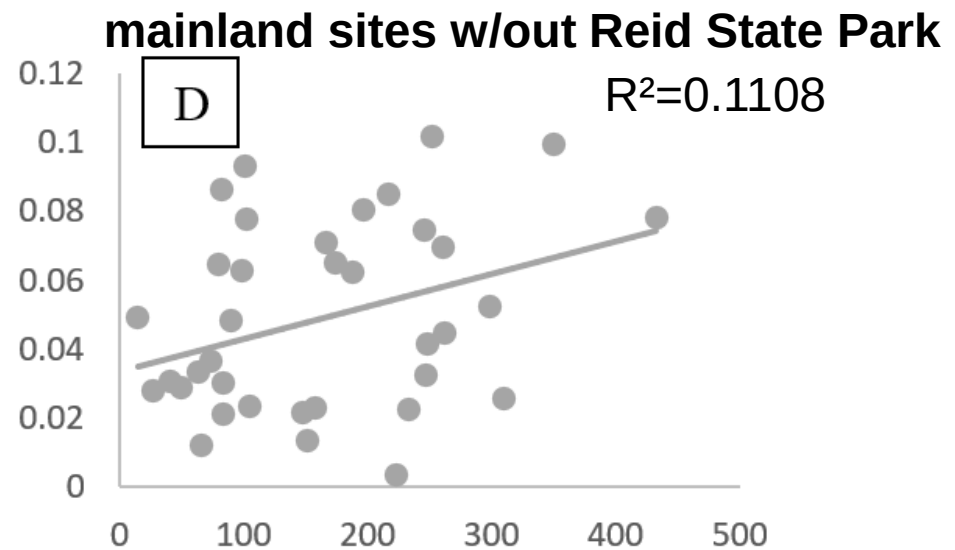
Pairwise distance (km)

# Chapter I: Genetic Divergence



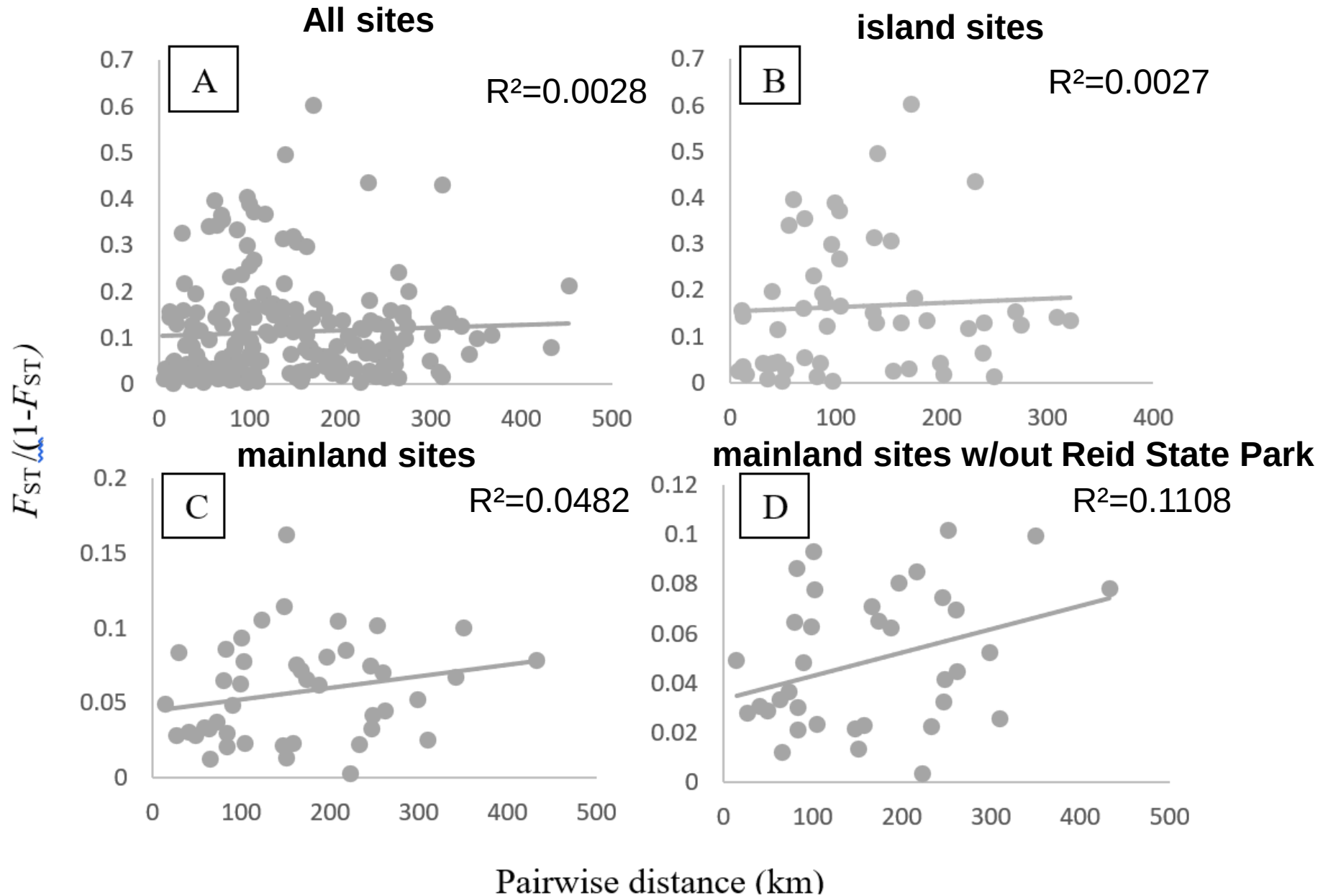
# Chapter I: Genetic Divergence

$$F_{ST} / (1 - F_{ST})$$

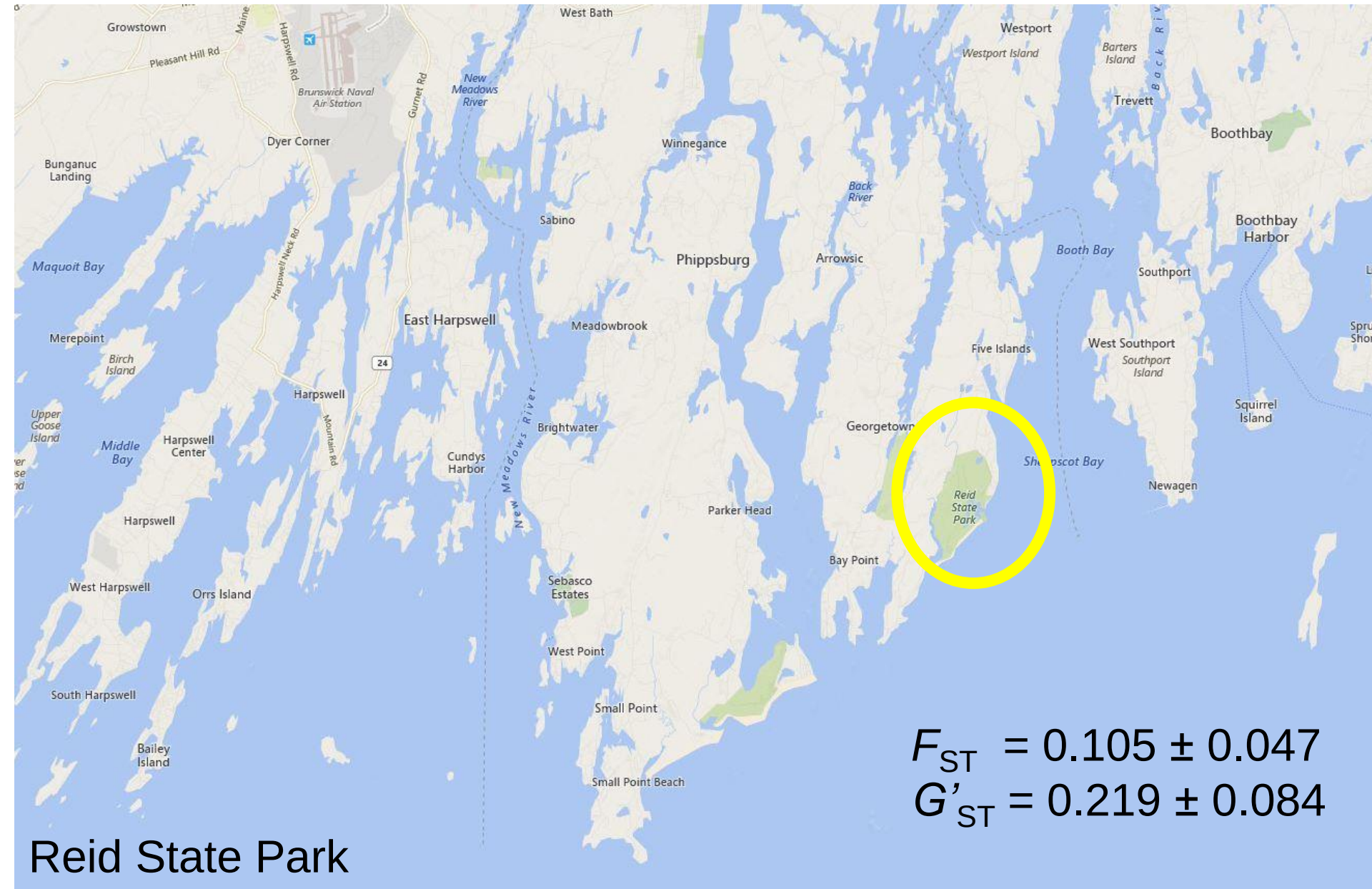


Pairwise distance (km)

# Chapter I: Genetic Divergence



# Chapter I: Genetic Divergence



$$F_{ST} = 0.105 \pm 0.047$$
$$G'_{ST} = 0.219 \pm 0.084$$

Reid State Park

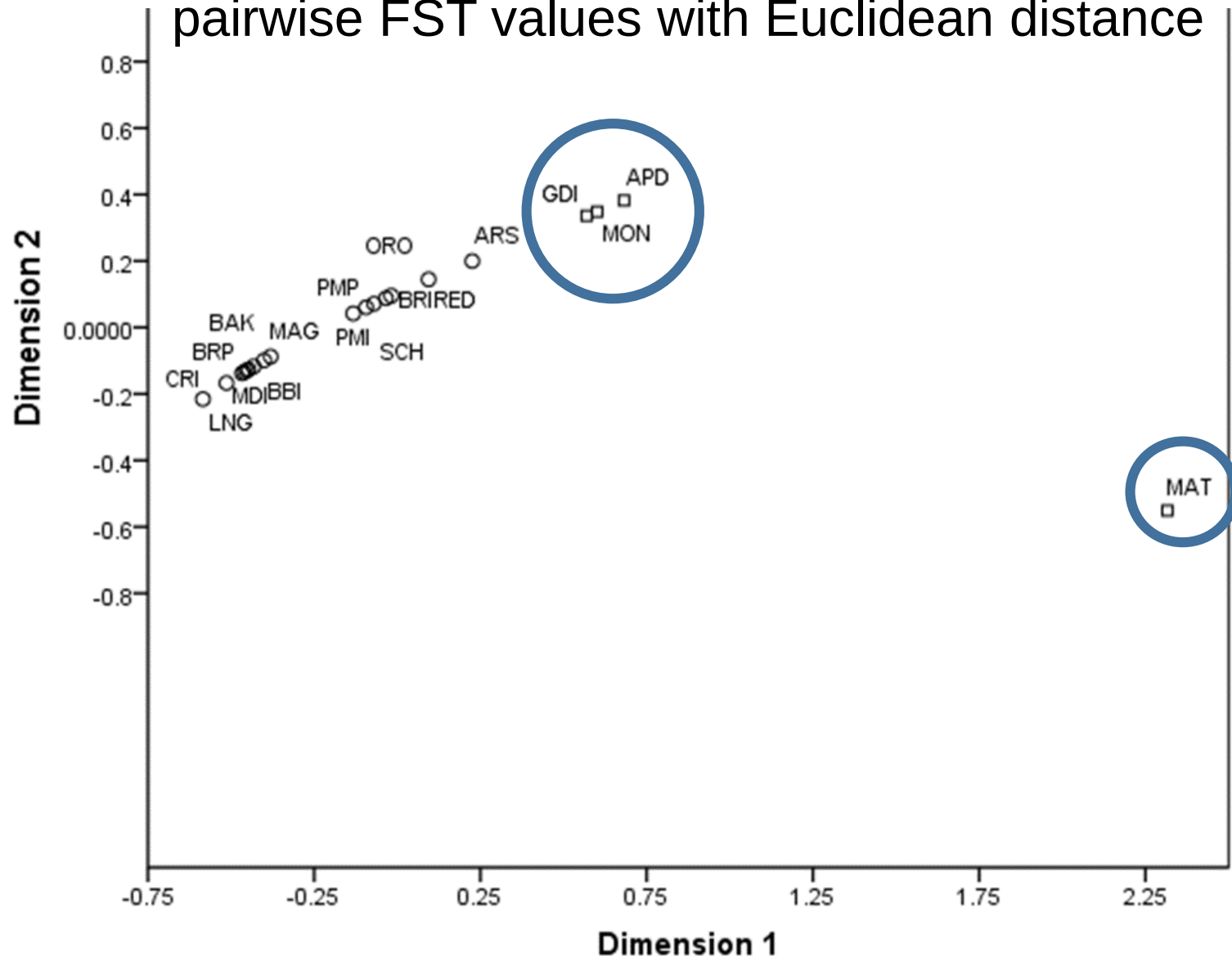
# Chapter I: Genetic Diversity

| Site | Sample Size<br>$n$ | Mean number<br>of alleles<br>$k$ | Allelic richness<br>$A$ | $H_O$ | $H_E$ |
|------|--------------------|----------------------------------|-------------------------|-------|-------|
| APD  | 34                 | 4.11                             | 3.65                    | 0.529 | 0.522 |
| ARS  | 17                 | 5.11                             | 5.03                    | 0.627 | 0.635 |
| BAK  | 30                 | 6.33                             | 5.46                    | 0.667 | 0.691 |
| BBI  | 30                 | 6.88                             | 5.84                    | 0.707 | 0.732 |
| BRP  | 20                 | 5.33                             | 5.10                    | 0.672 | 0.681 |
| CRI  | 31                 | 6.11                             | 5.23                    | 0.692 | 0.714 |
| GDI  | 30                 | 4.88                             | 4.17                    | 0.570 | 0.578 |
| LNG  | 30                 | 6.44                             | 5.42                    | 0.637 | 0.686 |
| MAG  | 30                 | 7.11                             | 5.99                    | 0.685 | 0.701 |
| MAT  | 32                 | 3.88                             | 3.31                    | 0.392 | 0.416 |
| MON  | 30                 | 3.77                             | 3.44                    | 0.574 | 0.548 |
| MDI  | 19                 | 5.55                             | 5.35                    | 0.661 | 0.722 |
| ORO  | 20                 | 5.66                             | 5.41                    | 0.656 | 0.682 |
| PLC  | 24                 | 5.55                             | 5.00                    | 0.718 | 0.689 |
| PMI  | 37                 | 5.88                             | 5.09                    | 0.685 | 0.688 |
| PMP  | 16                 | 5.00                             | 5.00                    | 0.729 | 0.699 |
| RED  | 32                 | 6.55                             | 5.34                    | 0.563 | 0.606 |
| SCH  | 23                 | 5.66                             | 5.18                    | 0.715 | 0.690 |
| UMM  | 23                 | 5.77                             | 5.36                    | 0.671 | 0.703 |
| BRI  | 30                 | 5.77                             | 5.06                    | 0.670 | 0.657 |
| WLF  | 29                 | 6.11                             | 5.42                    | 0.724 | 0.677 |

Mean number of alleles: mainland 5.8, islands 5.42, distant islands 4.16

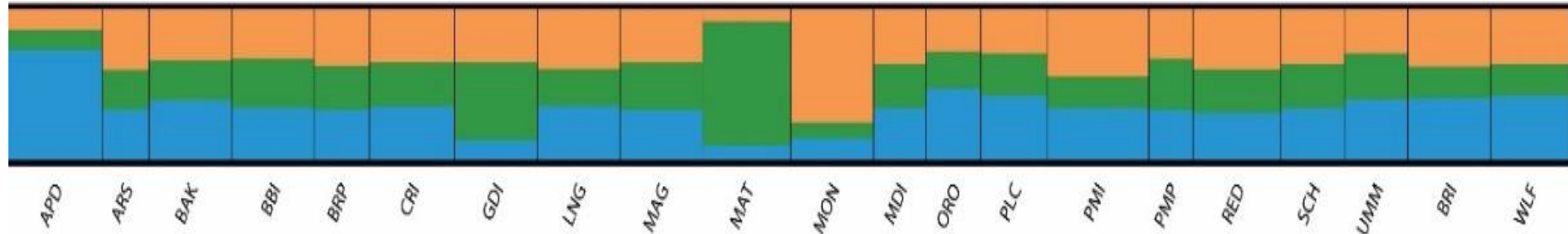
# Chapter I: Genetic Relatedness

- Nonmetric Multidimensional Scaling (NMDS) plot using pairwise  $F_{ST}$  values with Euclidean distance

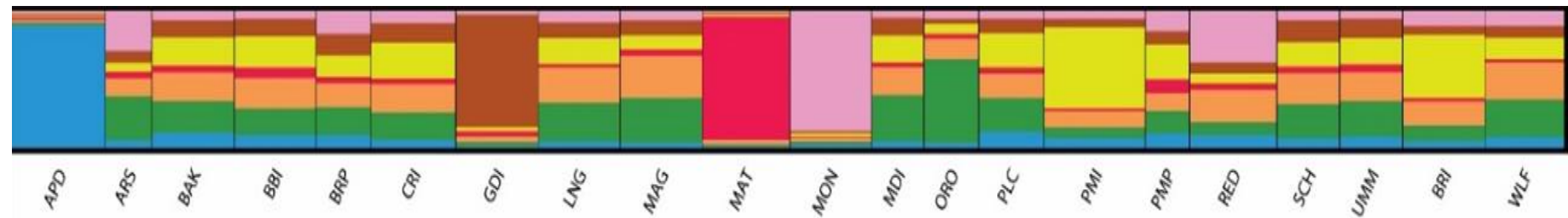


# Chapter I: Genetic Relatedness

- Structure analysis with no location prior

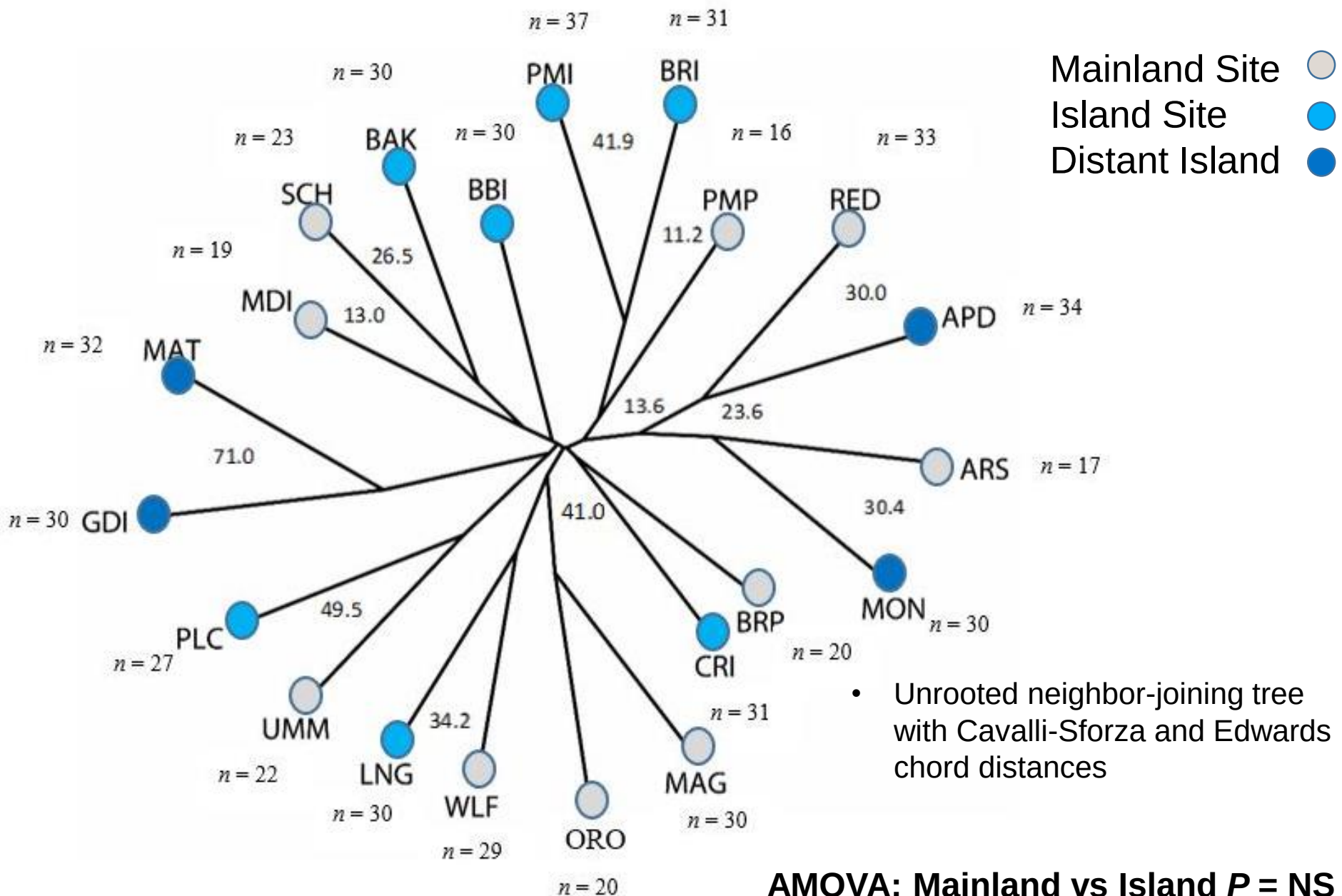


$K = 3$



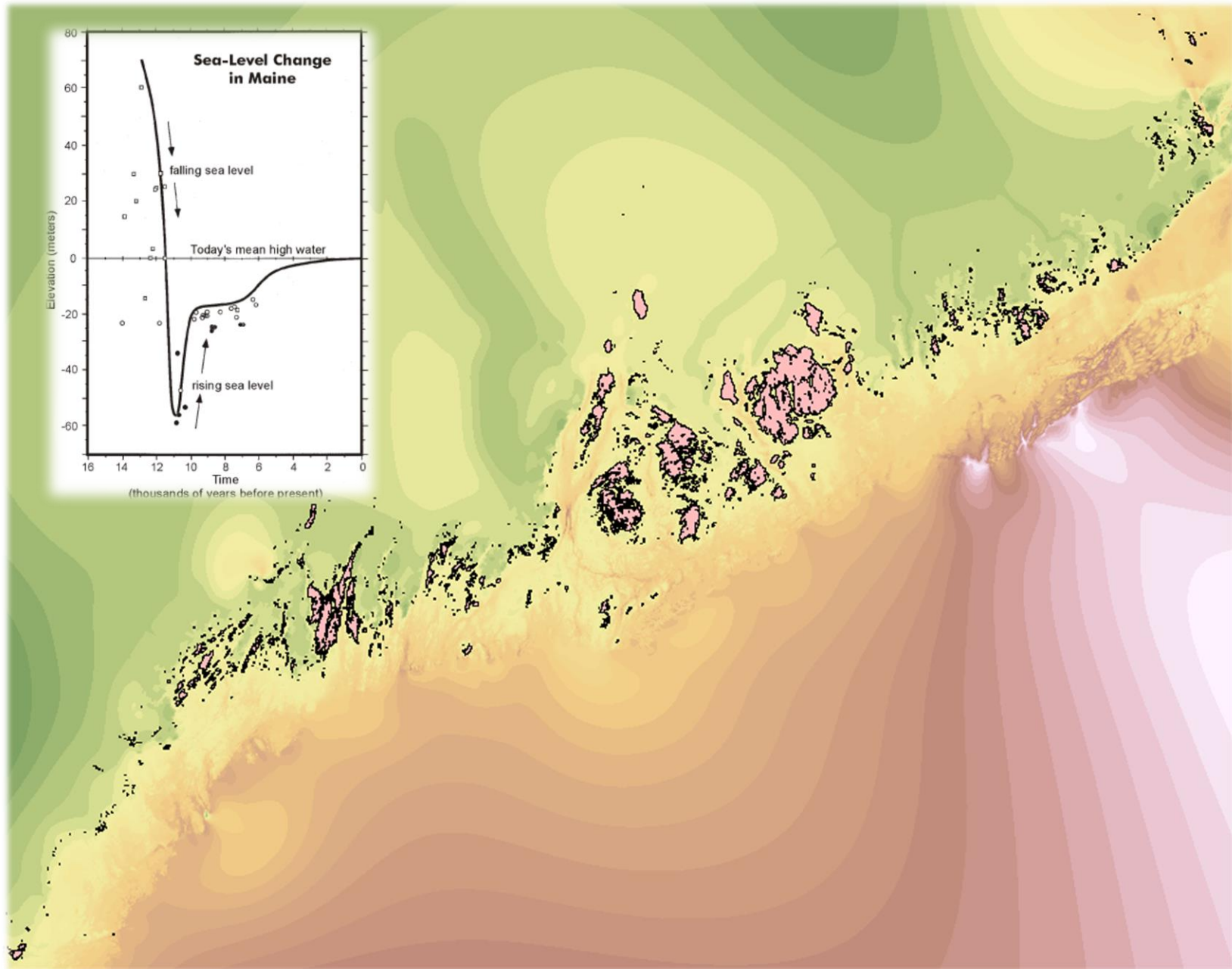
$K = 7$

# Chapter I: Genetic Relatedness



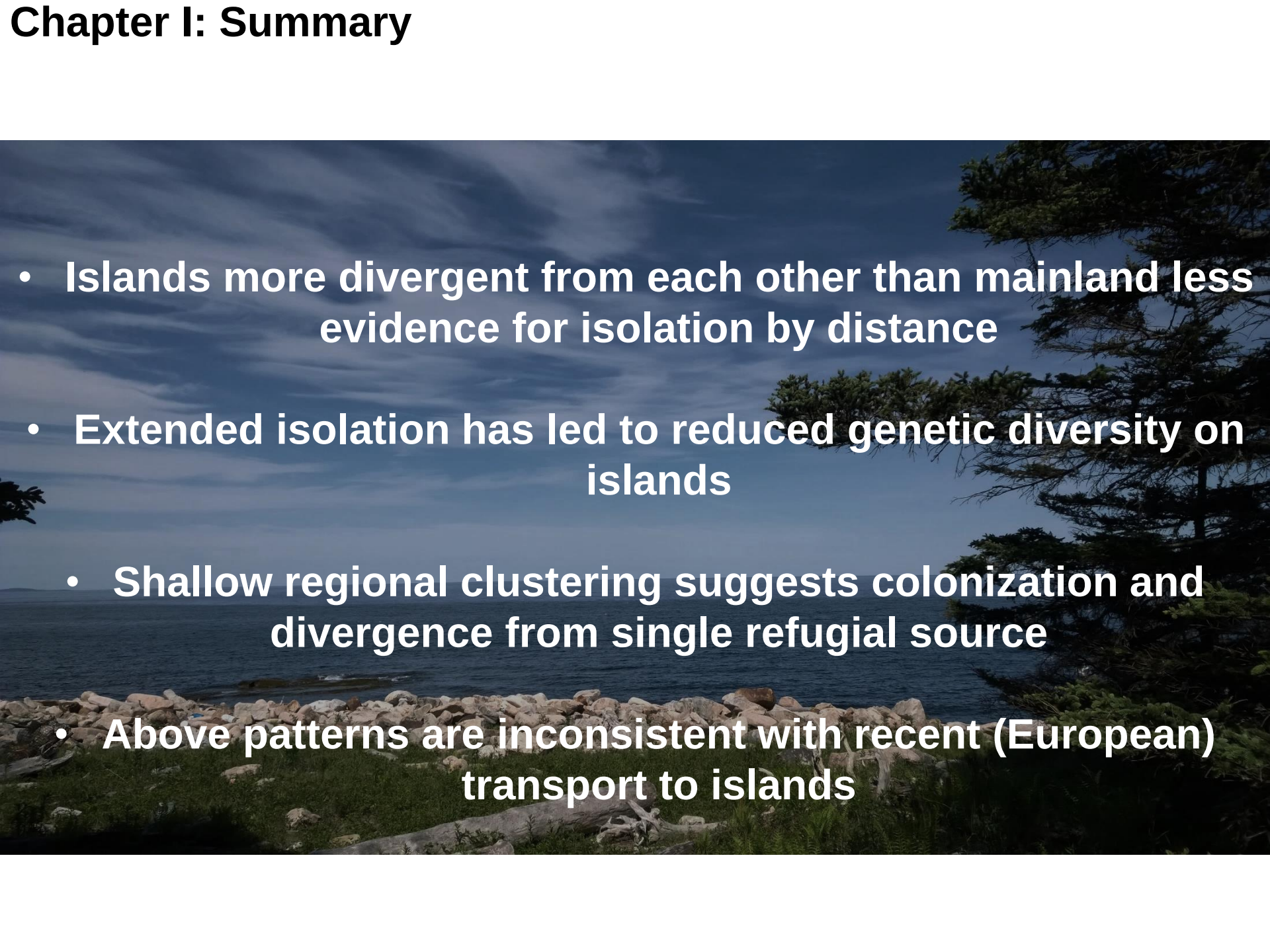
**AMOVA: Mainland vs Island  $P = \text{NS}$**   
**AMOVA: by Tree groupings  $P = <0.001$**

# Chapter I: Population Structure and Biogeographic Origins



| Chapter I: Population Structure and Biogeographic Origins |                           |                           |
|-----------------------------------------------------------|---------------------------|---------------------------|
| Estimated Years Before Present                            | Island                    | Distance from present day |
| (YBP)                                                     |                           | coastline (km)            |
| 10,000 YBP                                                | Matinicus Island          | 23                        |
| 10,000 YBP                                                | Monhegan Island           | 17                        |
| 9,000 YBP                                                 | Great Duck Island         | 10                        |
| 6,000 YBP                                                 | Appledore Island          | 10                        |
| 4,000 YBP                                                 | All Other Sampled Islands | 1-5                       |

# Chapter I: Summary

- 
- Islands more divergent from each other than mainland less evidence for isolation by distance
  - Extended isolation has led to reduced genetic diversity on islands
  - Shallow regional clustering suggests colonization and divergence from single refugial source
  - Above patterns are inconsistent with recent (European) transport to islands

# Outline

- I. Introduction to island biogeography
  - a. classic island biogeography
  - b. Maine's coastal islands
  - c. formation of contemporary islands
  - d. the island salamander system



- II. Chapter I: Population Structure and Biogeographic Origins

- III. Chapter II: Trophic Ecology and Morphological Variation



- IV. Summary of Results, Research Significance, and Management Implications

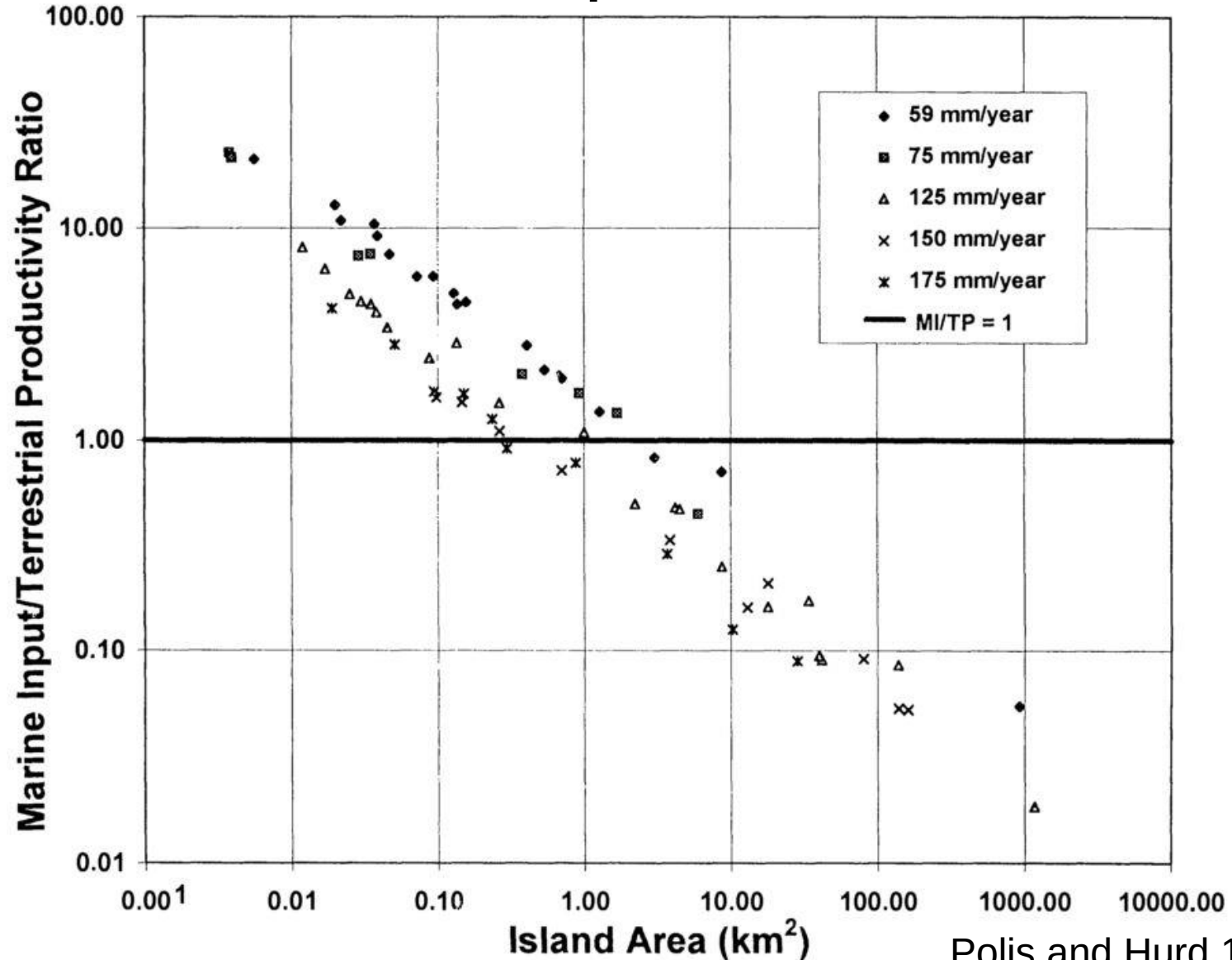


## Chapter II: Trophic Ecology and Morphological Variation



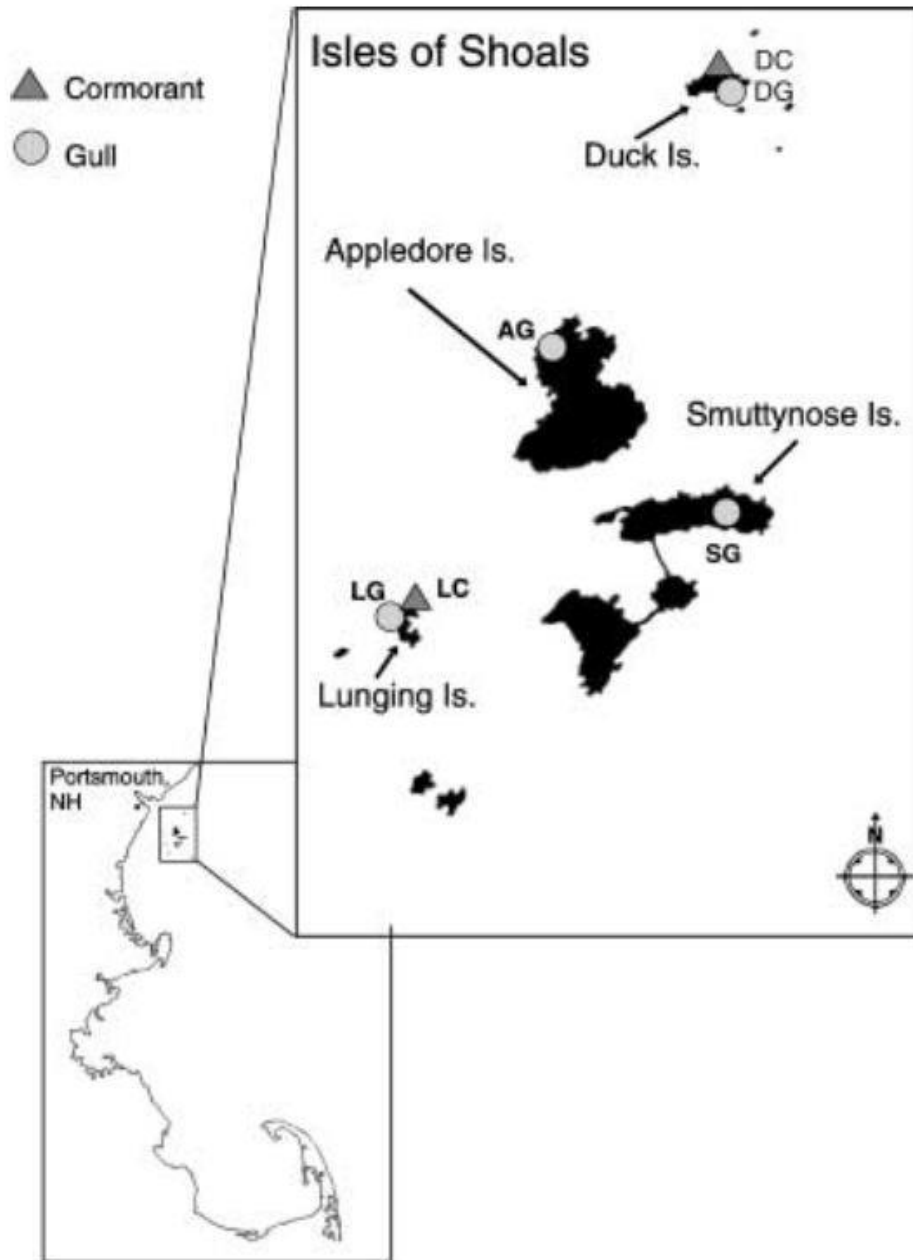
# Chapter II: Trophic Ecology and Morphological Variation

## Greater marine input for smaller islands



Polis and Hurd 1996

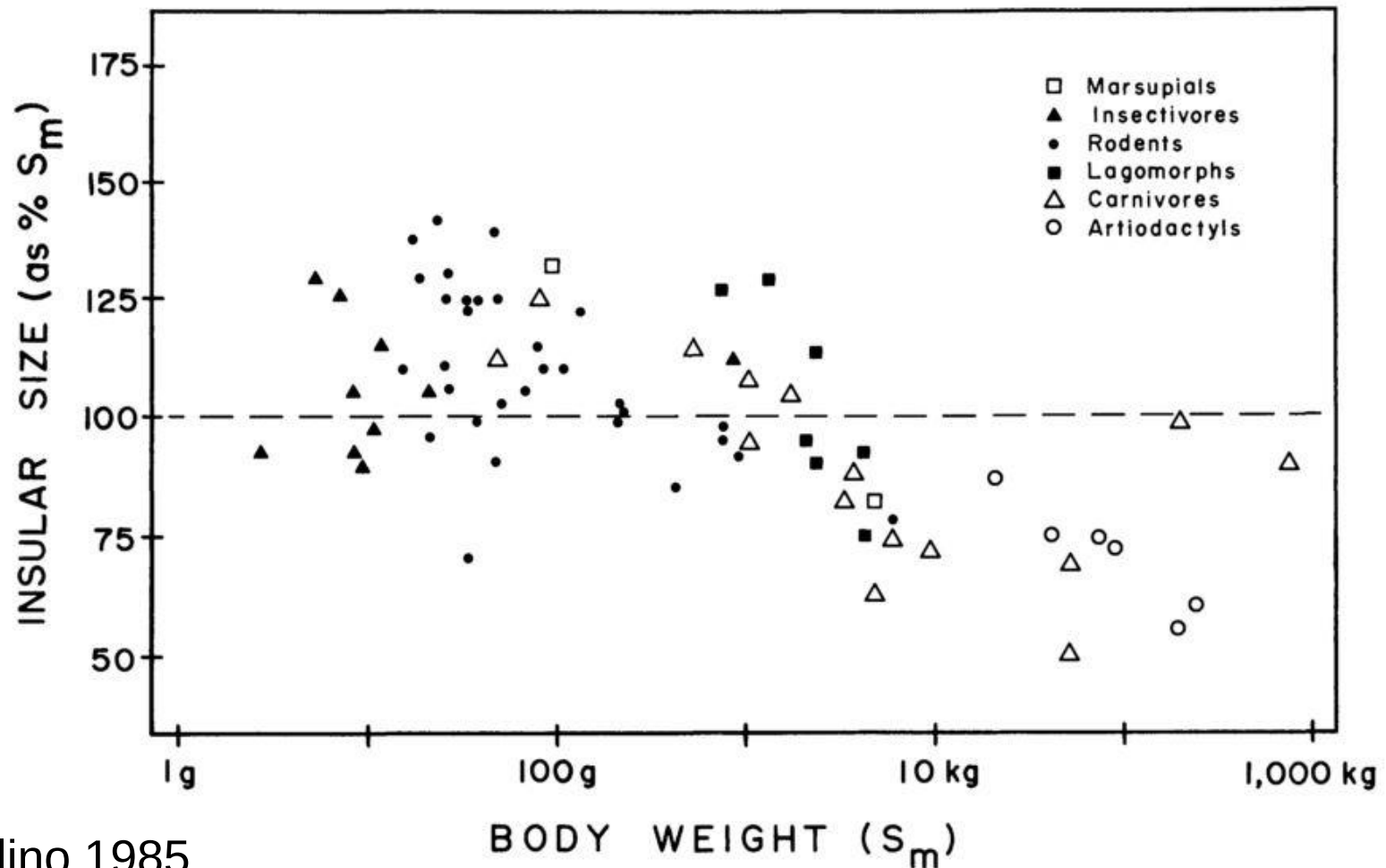
# Chapter II: Trophic Ecology and Morphological Variation



- Plants on seabird islands receive nutrient subsidies (Nitrogen)

# Chapter II: Trophic Ecology and Morphological Variation

**Body size: small animals get big and big animals get small**



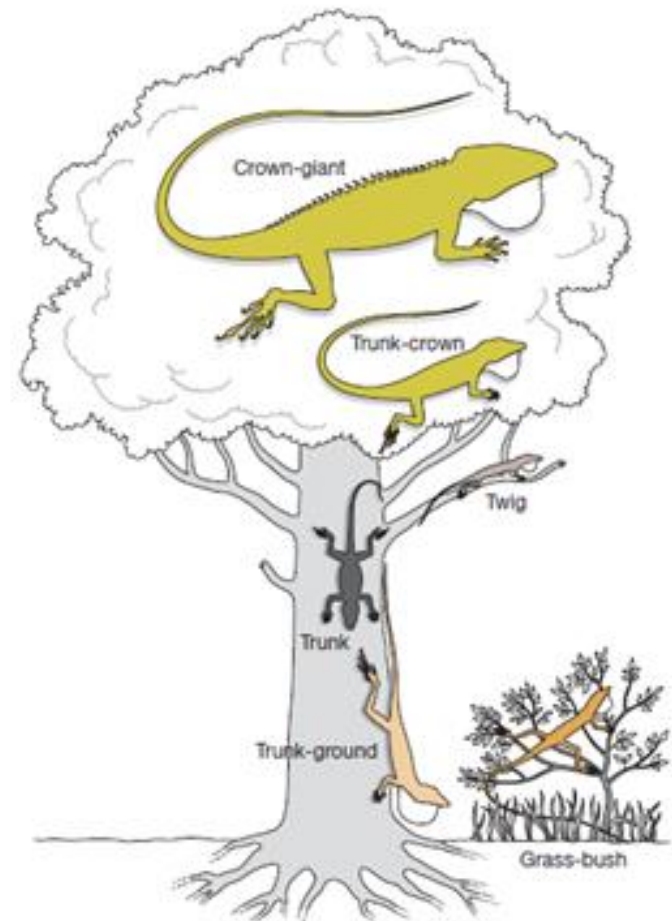
# Chapter II: Trophic Ecology and Morphological Variation

## Color



King 1993; King and Lawson 1997

## Body Shape



Losos 1990; Losos et al. 1997 and 1998

# Chapter II: Trophic Ecology and Morphological Variation



- Do island food webs receive C and N subsidies?
- Are island salamanders operating at higher trophic levels than their mainland counterparts?
- Is island habitat structure influencing morphological divergence?

# Chapter II: Trophic Ecology and Morphological Variation

- Stable isotopes of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) are an informative tool to infer food web interactions and trophic position

We expect:

$\delta^{13}\text{C}$

Primary production  
more marine



Primary production  
more terrestrial



$\delta^{15}\text{N}$

Subsidies  
more marine input



Per Trophic level  
3-4‰ per level



# Chapter II: Trophic Ecology and Morphological Variation

## trophic position estimation

$$\text{Trophic position} = \lambda + (\delta^{15}\text{N}_{\text{sc}} - \delta^{15}\text{N}_{\text{base}})/\Delta_n$$



$$\lambda = 1$$

$\lambda$  = trophic position of baseline organism

$\delta^{15}\text{N}_{\text{sc}}$  =  $\delta^{15}\text{N}$  of secondary consumer

$\delta^{15}\text{N}_{\text{base}}$  =  $\delta^{15}\text{N}$  of baseline organism

$\Delta_n$  = enrichment of  $\delta^{15}\text{N}$  per trophic level

(Estimated to be 3-4‰)

# Chapter II: Trophic Ecology and Morphological Variation

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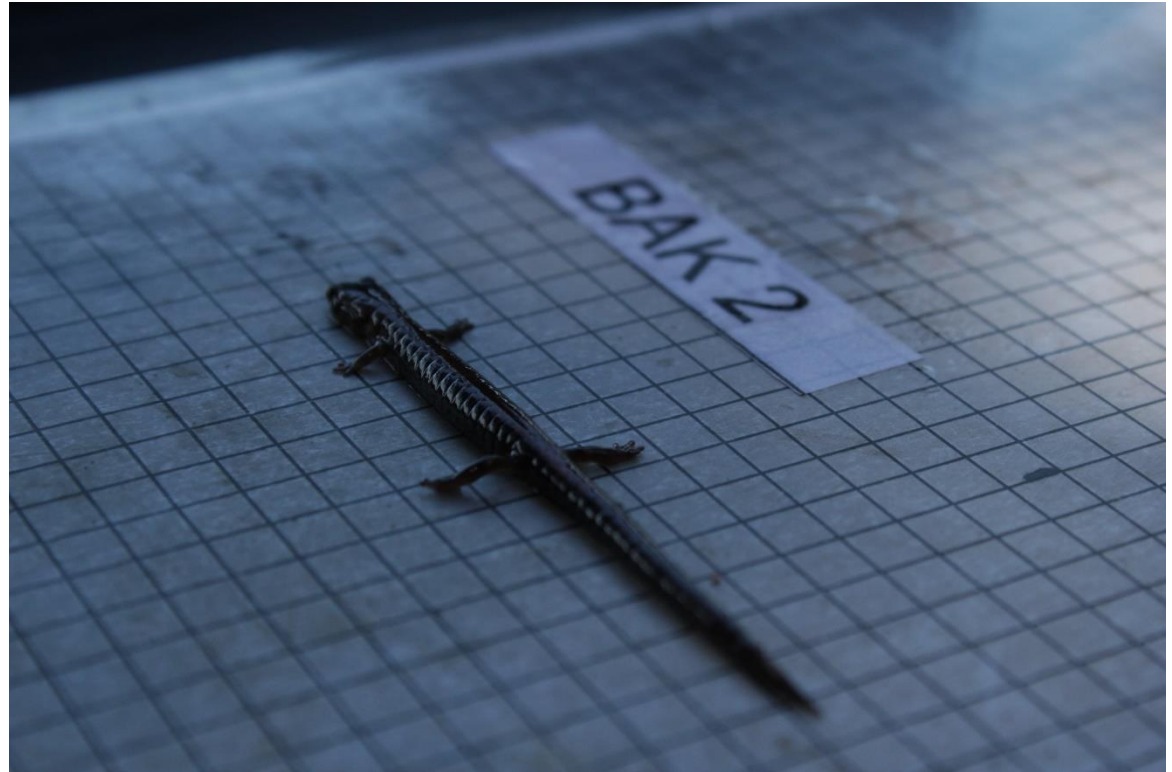
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$\Delta_n$  = enrichment of  $\delta^{15}\text{N}$  per trophic level

(Estimated to be 3-4‰)

# Chapter II: Trophic Ecology and Morphological Variation

- Dorsal and Ventral photographs
  - Snout Vent Length, Mass
    - 5 lethal salamander samples per site
- Isotopic baselines



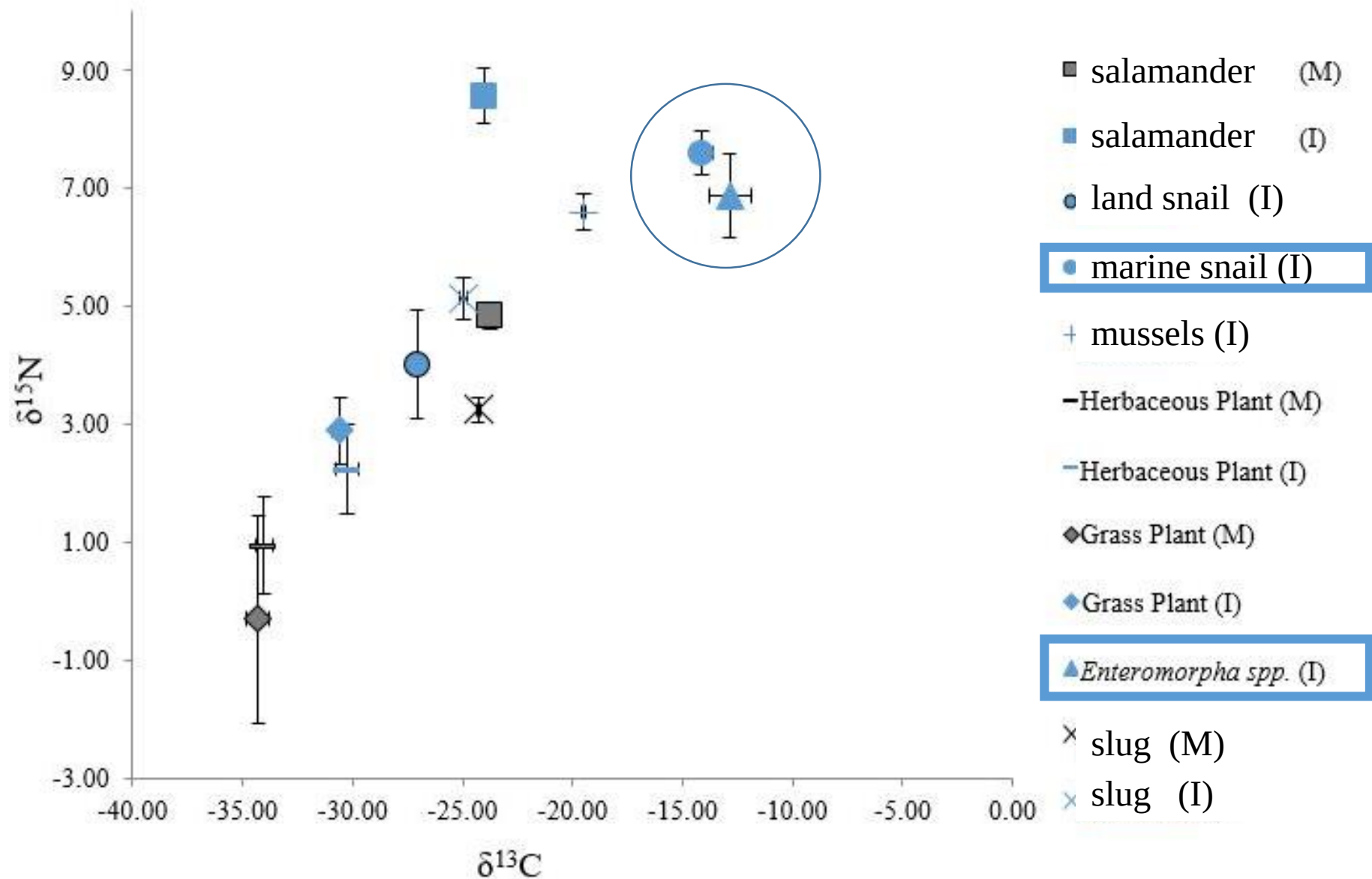
# Chapter II: Trophic Ecology and Morphological Variation

## Stable isotopes preparation

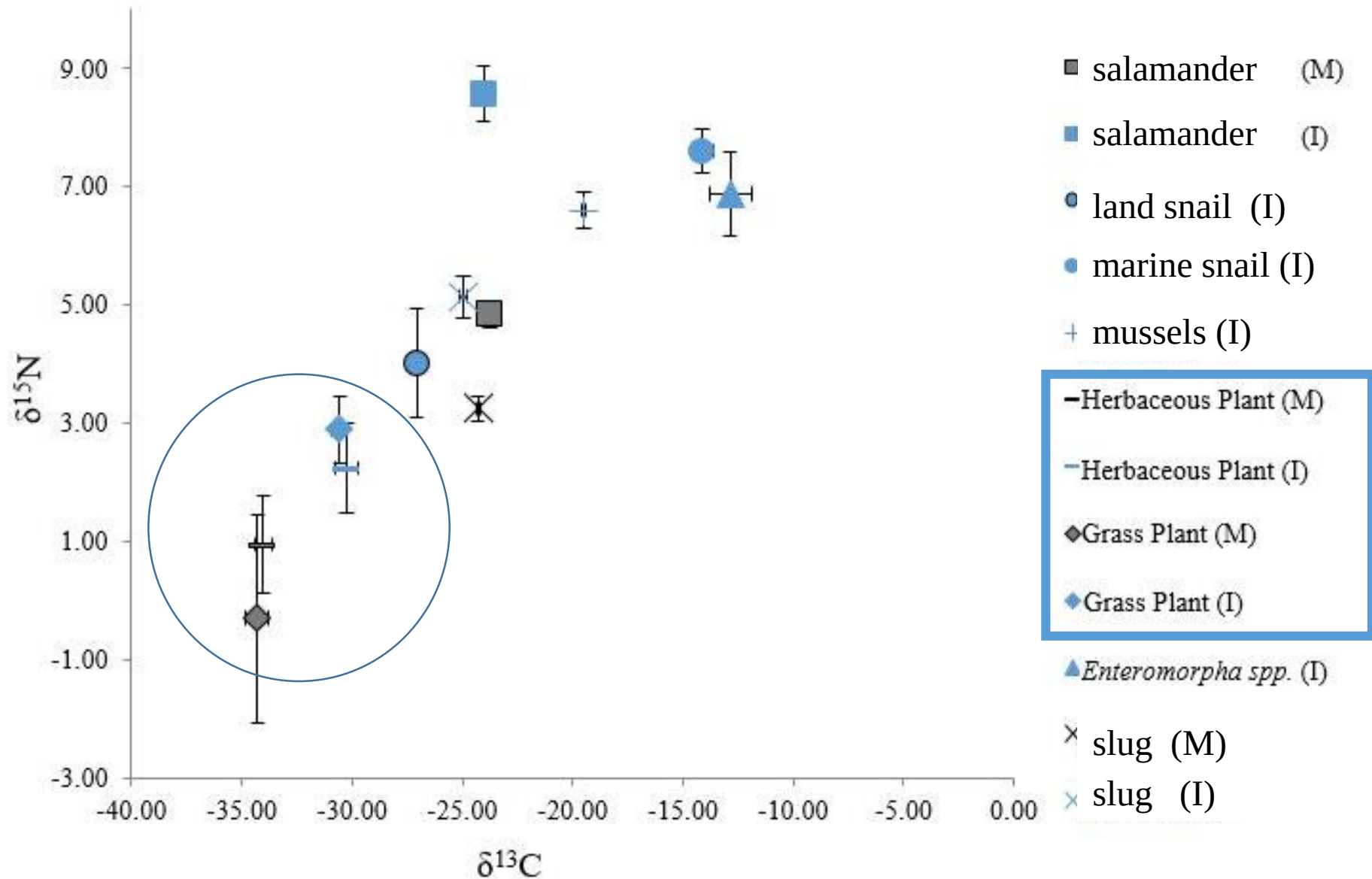
- Internal organs and tail removed to reduce potential bias
  - Tissue, dried, pulverized and homogenized
- Contents from 4 mainland sites and 6 island sites sent to UC Davis stable isotope facility



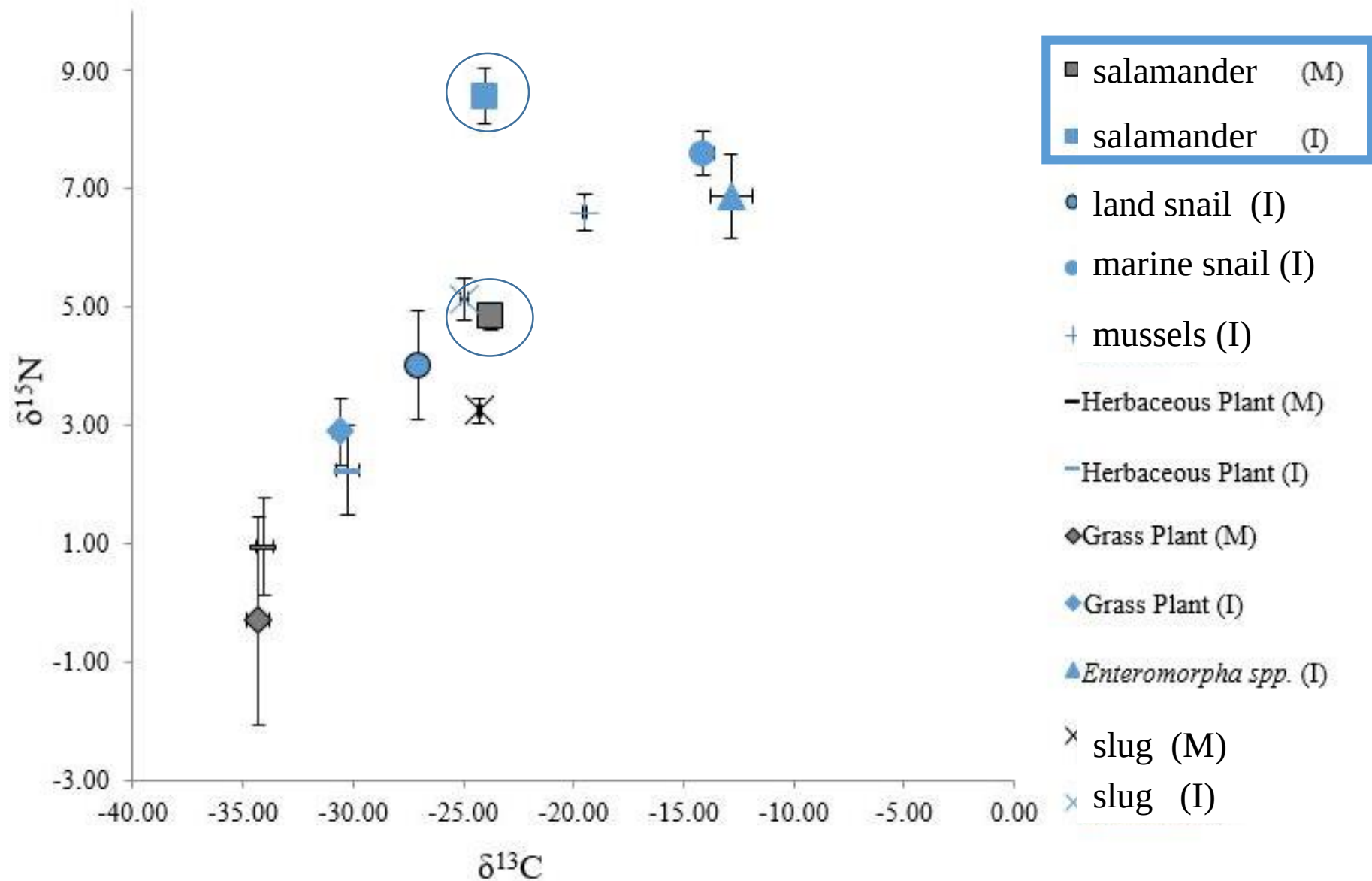
# Chapter II: Trophic Ecology and Morphological Variation



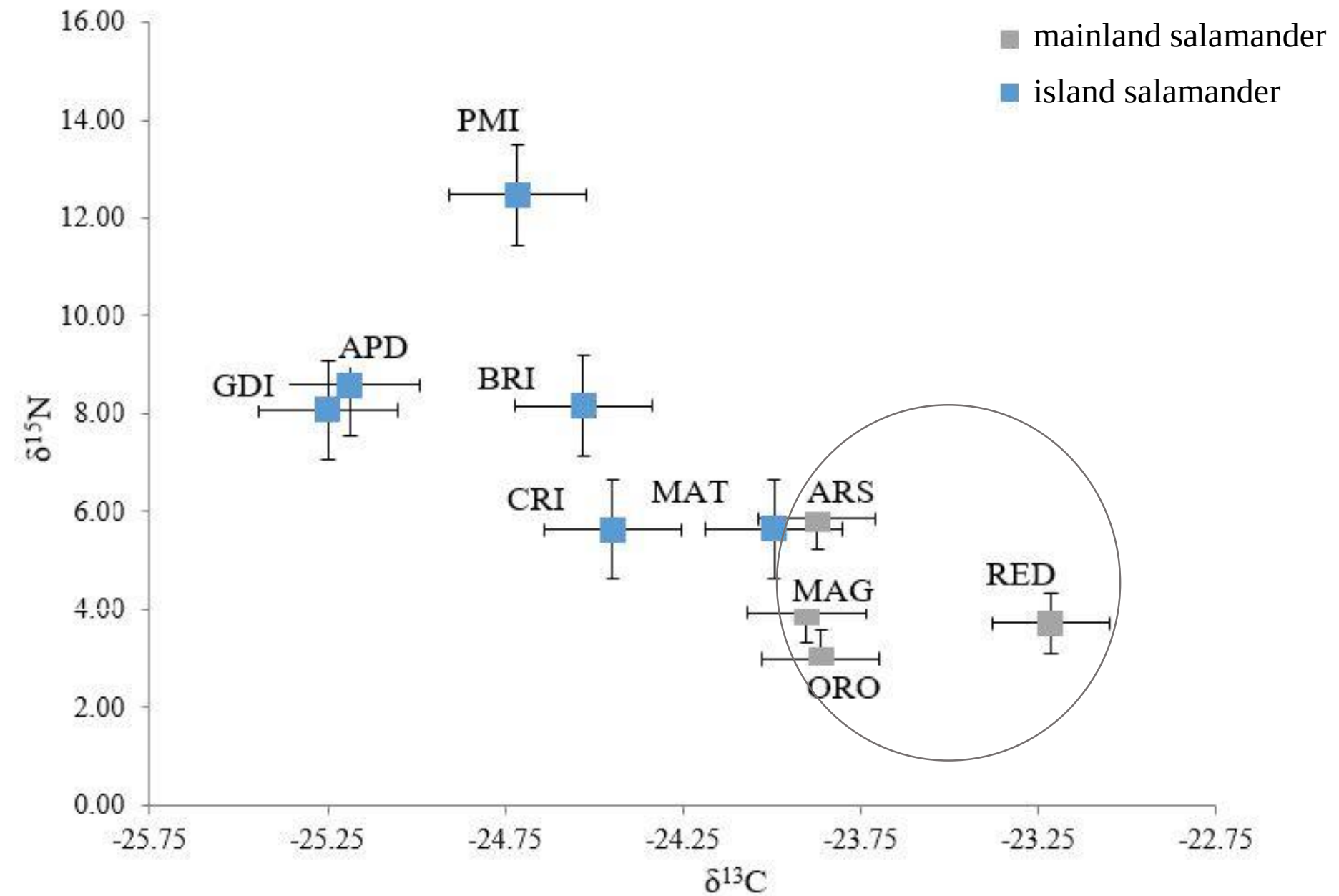
# Chapter II: Trophic Ecology and Morphological Variation



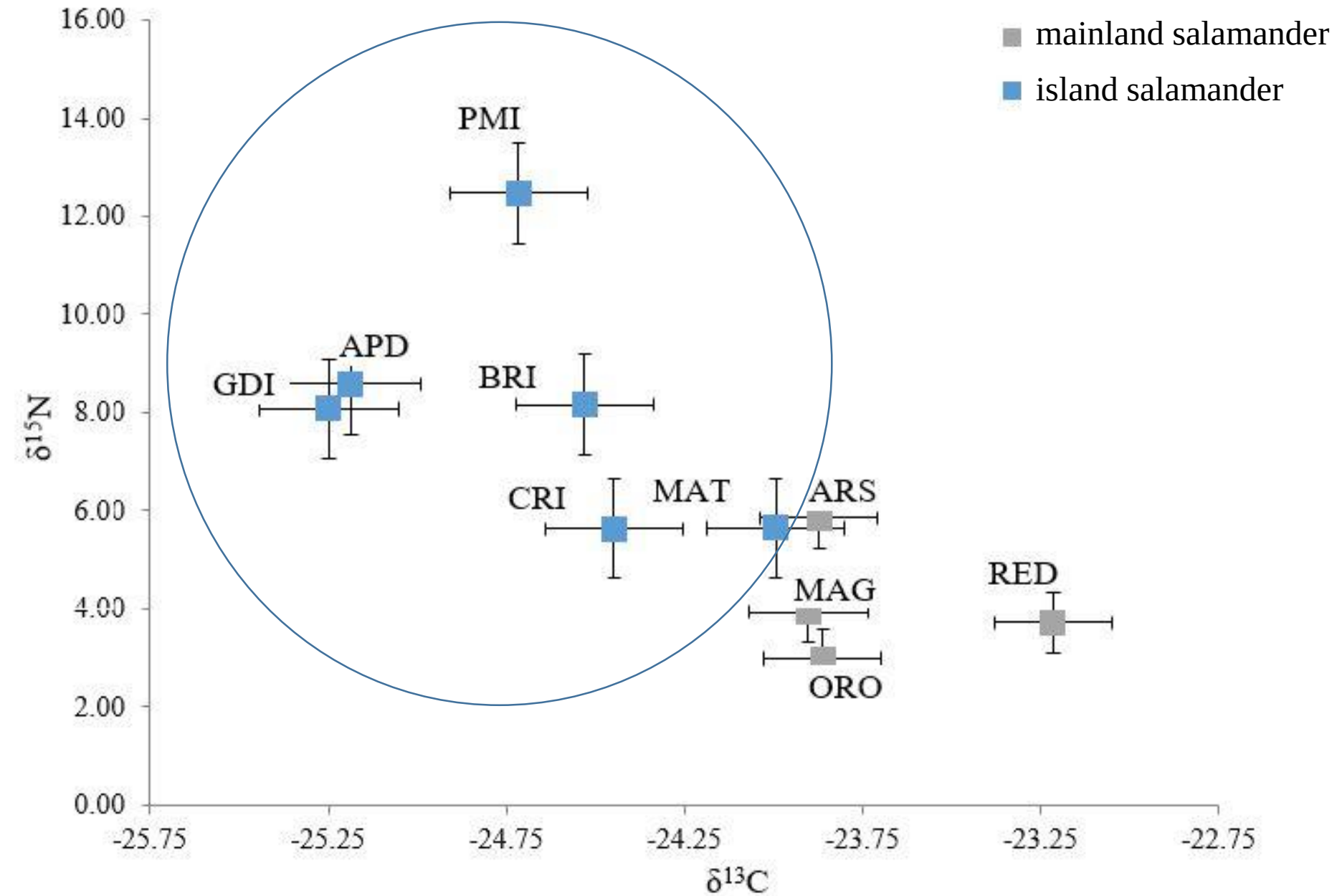
# Chapter II: Trophic Ecology and Morphological Variation



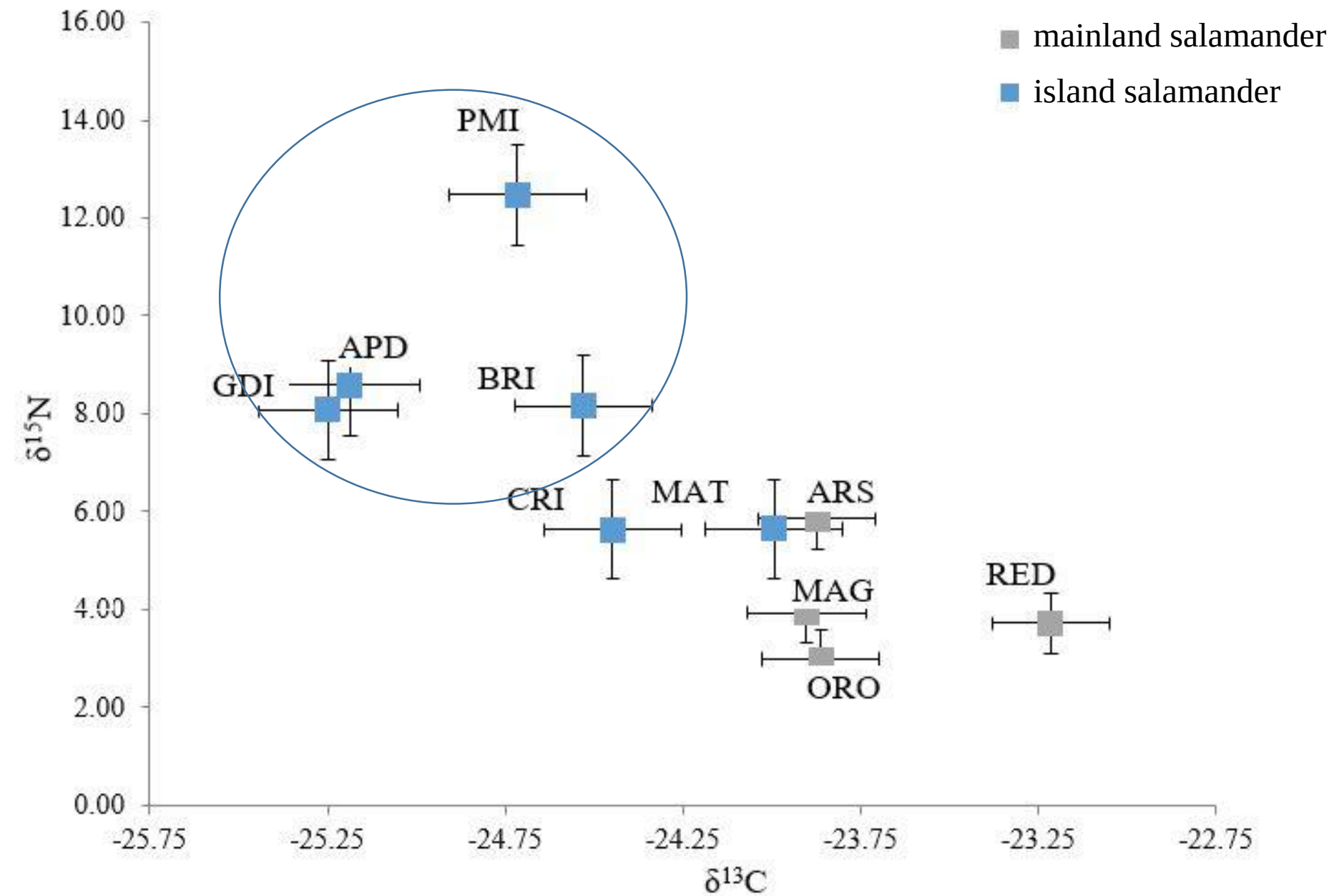
# Chapter II: Trophic Ecology and Morphological Variation



# Chapter II: Trophic Ecology and Morphological Variation



# Chapter II: Trophic Ecology and Morphological Variation



# Chapter II: Trophic Ecology and Morphological Variation

| Isotopic Feature      | Source                         | df | SS     | <i>F</i> | <i>P</i>  |
|-----------------------|--------------------------------|----|--------|----------|-----------|
| $\delta^{15}\text{N}$ | Island vs. Mainland            | 1  | 206.81 | 180.98   | < 0.0001* |
|                       | Population within Habitat Type | 8  | 314.72 | 34.46    | < 0.0001* |
| $\delta^{13}\text{C}$ | Island vs. Mainland            | 1  | 13.69  | 45.85    | < 0.0001* |
|                       | Population within Habitat Type | 8  | 8.72   | 3.65     | 0.0016*   |
| Trophic Level         | Island vs. Mainland            | 1  | 4.82   | 48.89    | < 0.0001* |
|                       | Population within Habitat Type | 8  | 22.11  | 27.99    | < 0.0001* |

**$\delta^{15}\text{N}$  signatures of red-backed salamanders significantly differed between island/mainland and populations**

# Chapter II: Trophic Ecology and Morphological Variation

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**$\delta^{13}\text{C}$  signatures of red-backed salamanders significantly differed between island/mainland and populations**

# Chapter II: Trophic Ecology and Morphological Variation

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**Trophic level of red-backed salamanders significantly differed between island/mainland and populations**

# Chapter II: Trophic Ecology and Morphological Variation

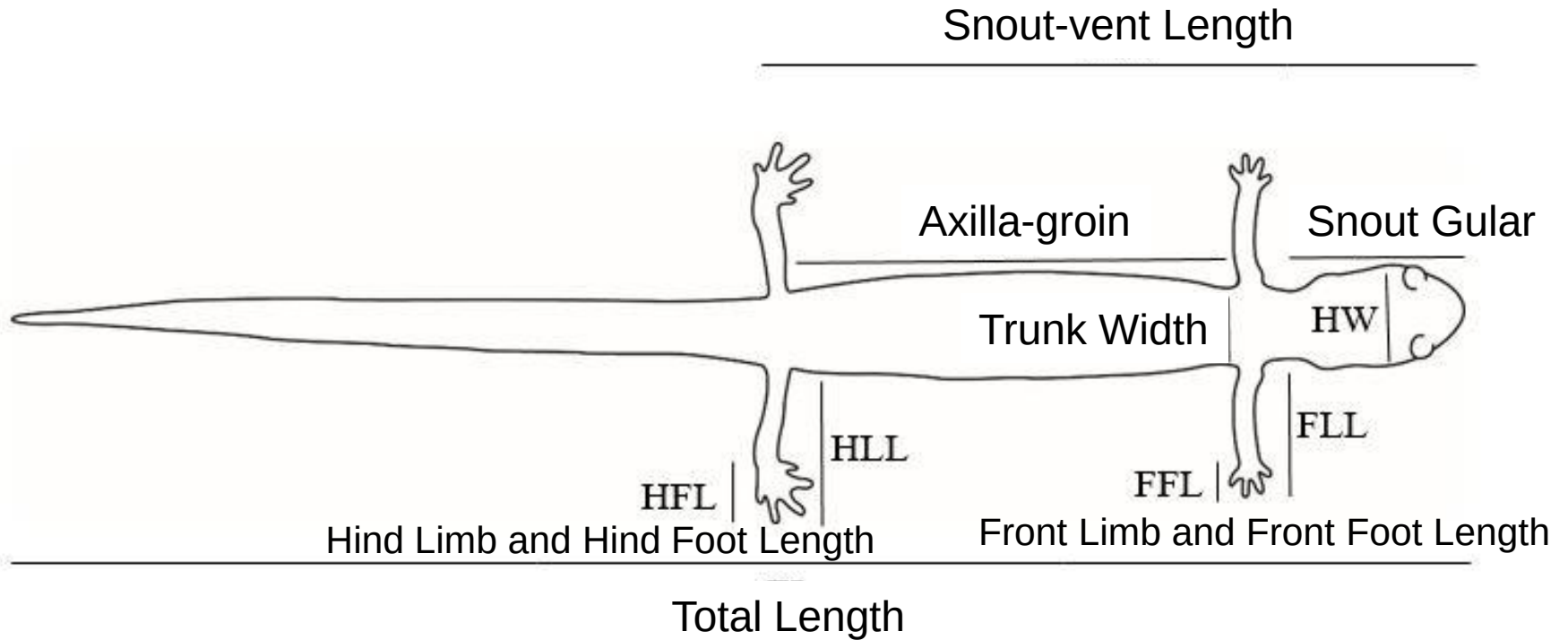
## Trophic position

| Site       | Site Type     | Trophic Position ( $\pm$ SD)       |
|------------|---------------|------------------------------------|
| ARS        | Mainland      | $2.19 \pm 0.183$                   |
| MAG        | Mainland      | $1.93 \pm 0.388$                   |
| ORO        | Mainland      | $1.55 \pm 0.258$                   |
| RED        | Mainland      | $2.54 \pm 0.242$                   |
| <b>APD</b> | <b>Island</b> | <b><math>2.87 \pm 0.140</math></b> |
| <b>BRI</b> | <b>Island</b> | <b><math>3.24 \pm 0.205</math></b> |
| CRI        | Island        | $1.83 \pm 0.217$                   |
| <b>GDI</b> | <b>Island</b> | <b><math>3.75 \pm 0.665</math></b> |
| MAT        | Island        | $2.28 \pm 0.242$                   |
| <b>PMI</b> | <b>Island</b> | <b><math>3.18 \pm 0.372</math></b> |

Island salamanders feeding at higher mean trophic levels

**Especially smaller islands with seabird colonies**

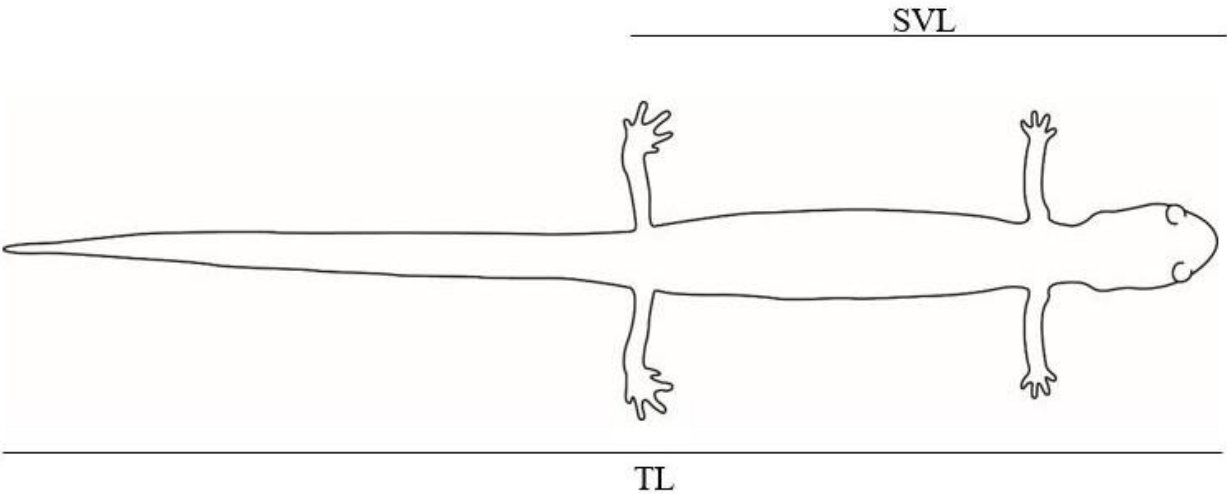
# Chapter II: Trophic Ecology and Morphological Variation



# Chapter II: Trophic Ecology and Morphological Variation

## Size Variation

| Size Trait | Source                         | df | SS       | <i>F</i> | <i>P</i>  |
|------------|--------------------------------|----|----------|----------|-----------|
| TL         | Island vs. Mainland            | 1  | 7065     | 39.43    | < 0.0001* |
|            | Population within Habitat Type | 20 | 43092    | 12.02    | < 0.0001* |
| SVL        | Island vs. Mainland            | 1  | 1699     | 50.49    | < 0.0001* |
|            | Population within Habitat Type | 20 | 9092     | 13.51    | < 0.0001* |
| Mass       | Island vs. Mainland            | 1  | 9549899  | 74.74    | < 0.0001* |
|            | Population within Habitat Type | 20 | 52259421 | 20.45    | < 0.0001* |



# Chapter II: Trophic Ecology and Morphological Variation

## Insular Gigantism



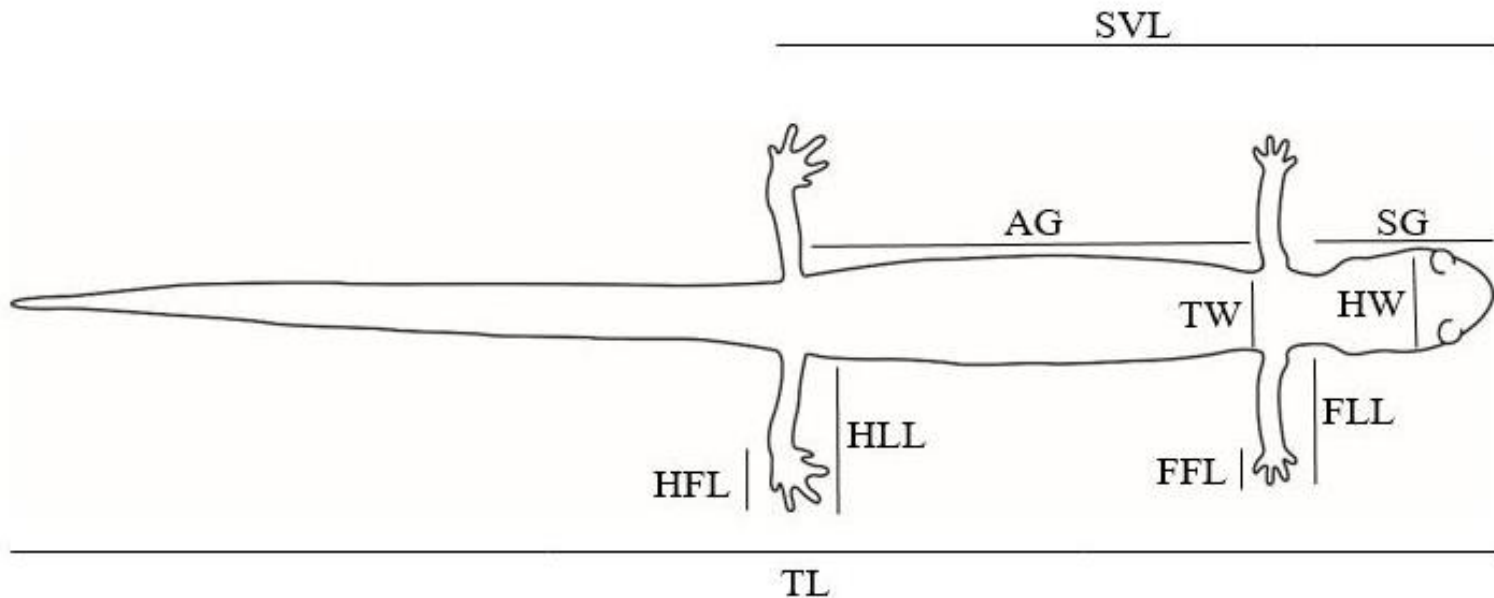
- Island salamander populations: 35% heavier, 8% longer SVL
- Largest salamanders collected from Petit Manan Island and Western Brothers Island

# Chapter II: Trophic Ecology and Morphological Variation

## Trait allometry and divergence

$$\log_{10}\text{Trait} = \log_{10}\text{SVL} + \text{Population (fixed)} + \log_{10}\text{SVL} * \text{Population}$$

- AG only trait to NOT significantly differ between populations relative to body size ( $P=0.0905$ )

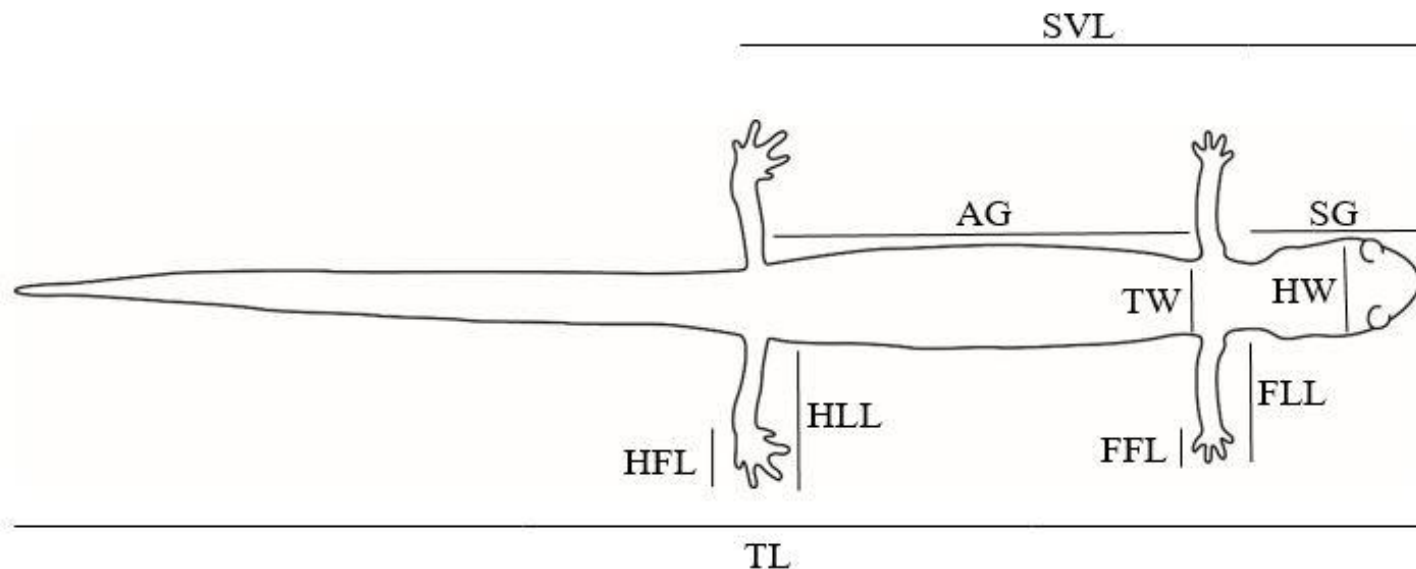


# Chapter II: Trophic Ecology and Morphological Variation

## Trait allometry and divergence

$\log \text{Trait} = \log_{10} \text{SVL} + \text{Habitat Type (fixed)} + \text{Population}$   
[random nested within Habitat Type] +  $\log_{10} \text{SVL} * \text{Habitat Type}$

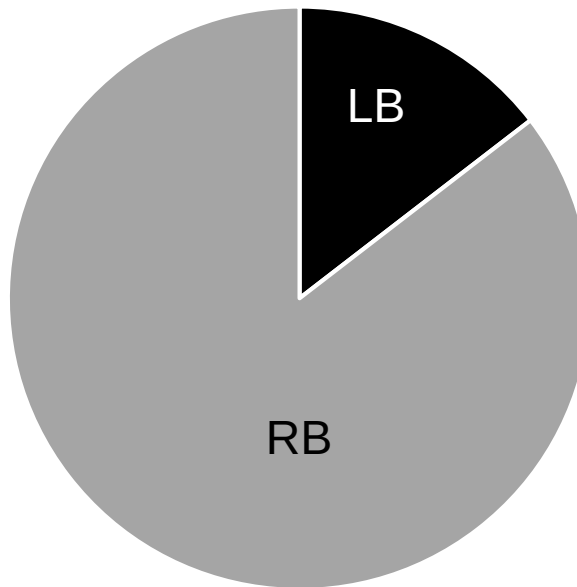
- Island populations featured larger head proportions (SG) for their body size ( $P = 0.0393$ )



# Chapter II: Trophic Ecology and Morphological Variation

## Color phase proportions

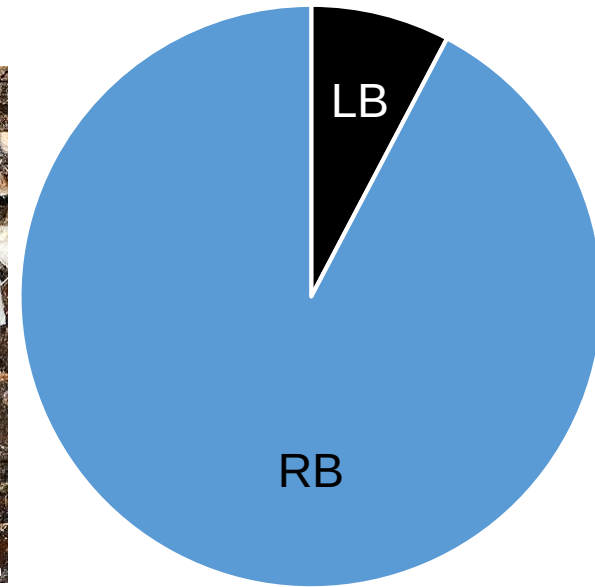
Mainland



39/229



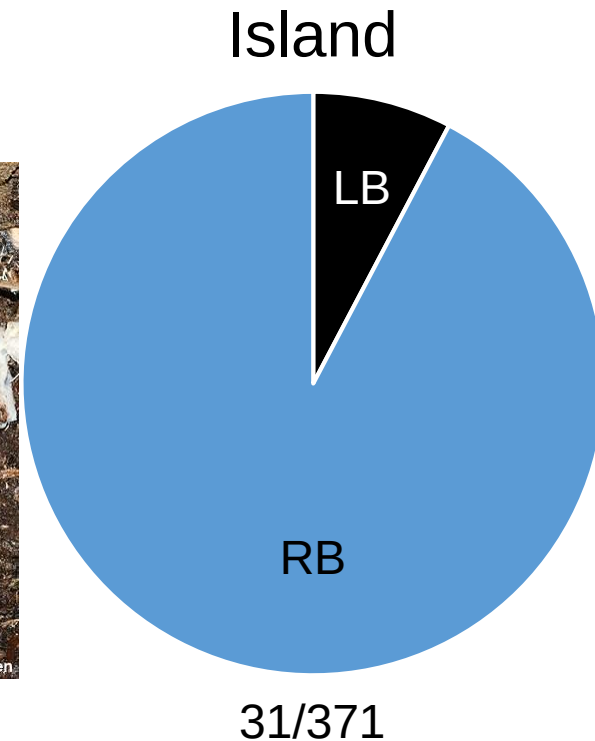
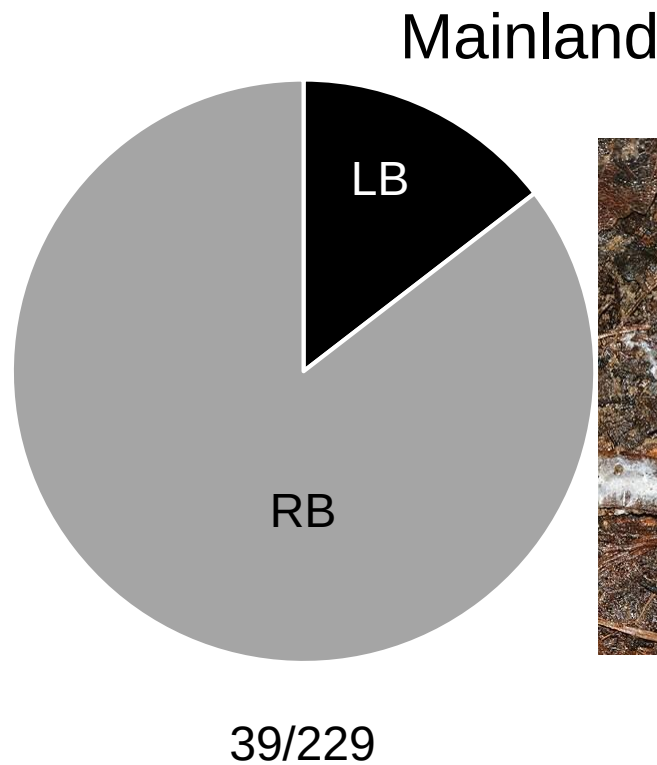
Island



31/371

# Chapter II: Trophic Ecology and Morphological Variation

## Color phase proportions



**55% of samples collected from Reid State Park were lead-backed**

# Chapter II: Trophic Ecology and Morphological Variation



- Island ecosystems depended mostly on terrestrial primary production, but experienced notable nitrogen subsidies (seabirds)
- Populations showed trait divergence: island salamanders had larger body size and relative head sizes

# Outline

- I. Introduction to island biogeography
  - a. classic island biogeography
  - b. Maine's coastal islands
  - c. formation of contemporary islands
  - d. the island salamander system



- II. Chapter I: Population Structure and Biogeographic Origins

- III. Chapter II: Trophic Ecology and Morphological Variation



- IV. Summary of Results, Research Significance, and Management Implications



# Summary

## Chapter I

- **extensive genetic differentiation across most distant sites**
- **regional clustering suggesting colonization from single refugial source**
  - **reduced genetic diversity on islands**

## Chapter II

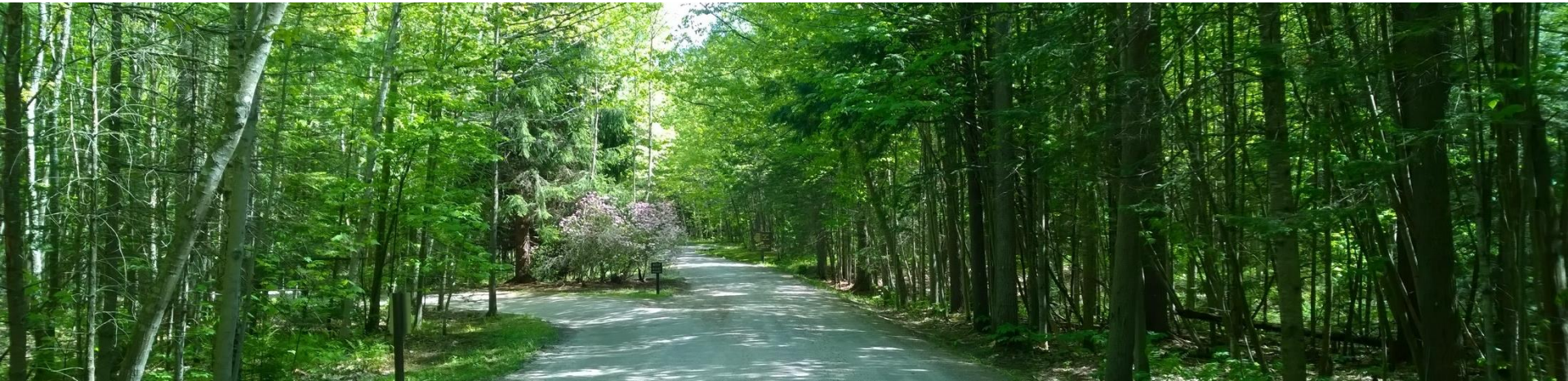
- **Island ecosystems receive increased nitrogen subsidies (seabirds)**
- **island salamanders are operating at higher trophic levels**
- **trait divergence: island salamanders had larger body size and relative head sizes**

# Novel Findings



- Isolated components of post-glacially derived variation
- Incipient stages of island adaptive radiations

# Management Implications



- Conservation of the common species
  - Seabird salamander relationship
  - Indicator of other cryptic diversity?



# Acknowledgements

## **Committee Members:**

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Roger Chandler

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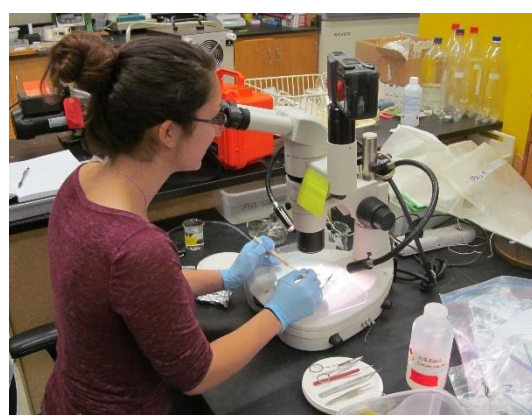
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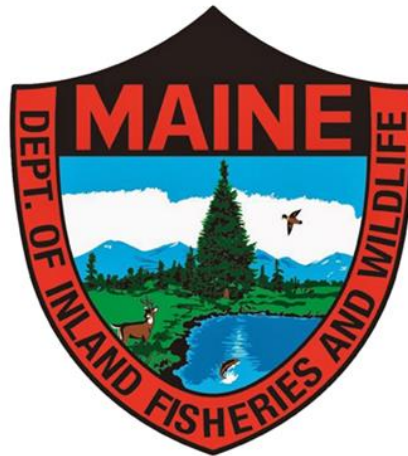
David Bridges



# Funding



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# Questions?

