# Quantifying nonlinear variations of thermal performance curves in evolutionary biology

**Rima Izem**

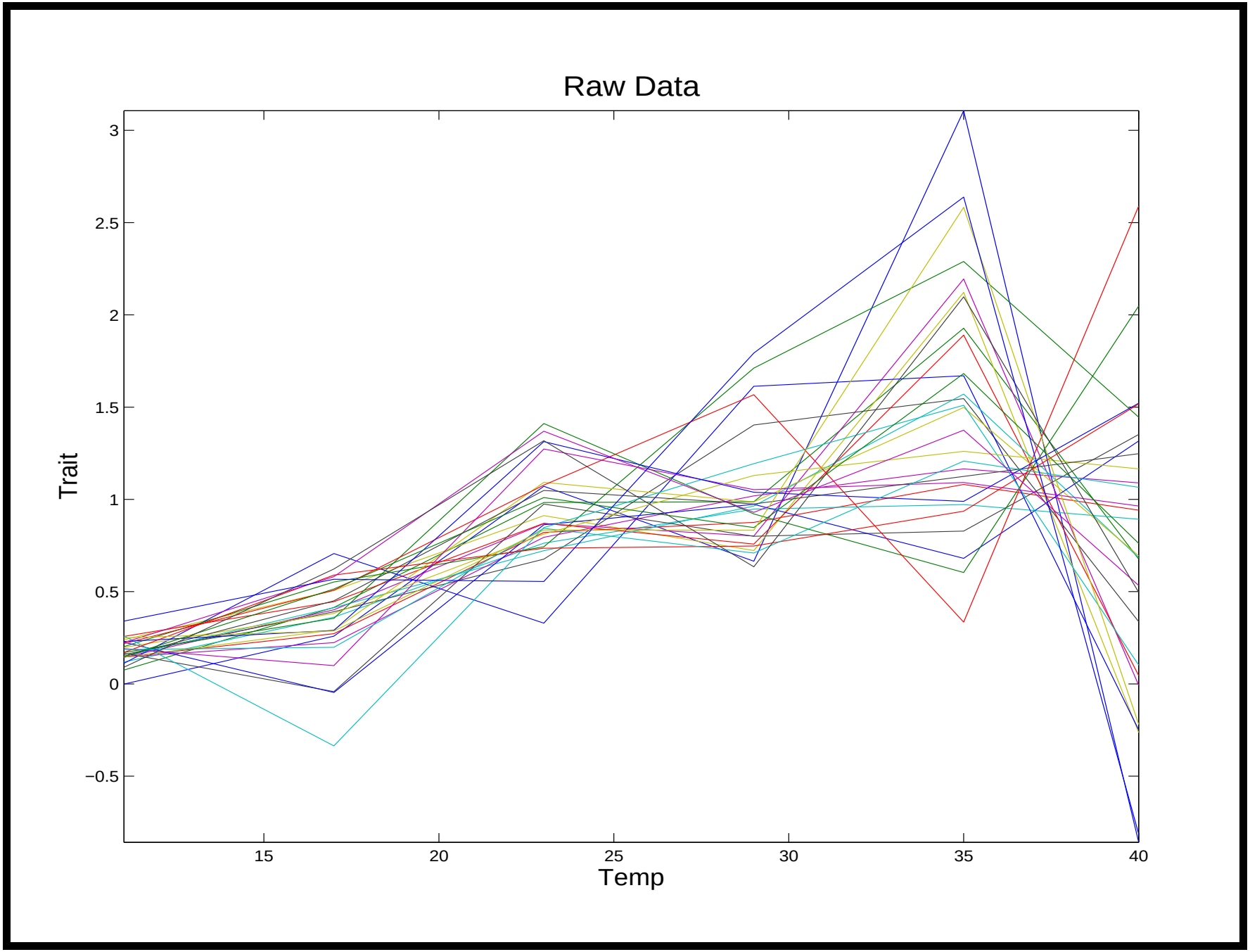
**Joint work with**

**J.S Marron, Department of Statistics**

**and**

**J.G Kingsolver, Department of Biology**

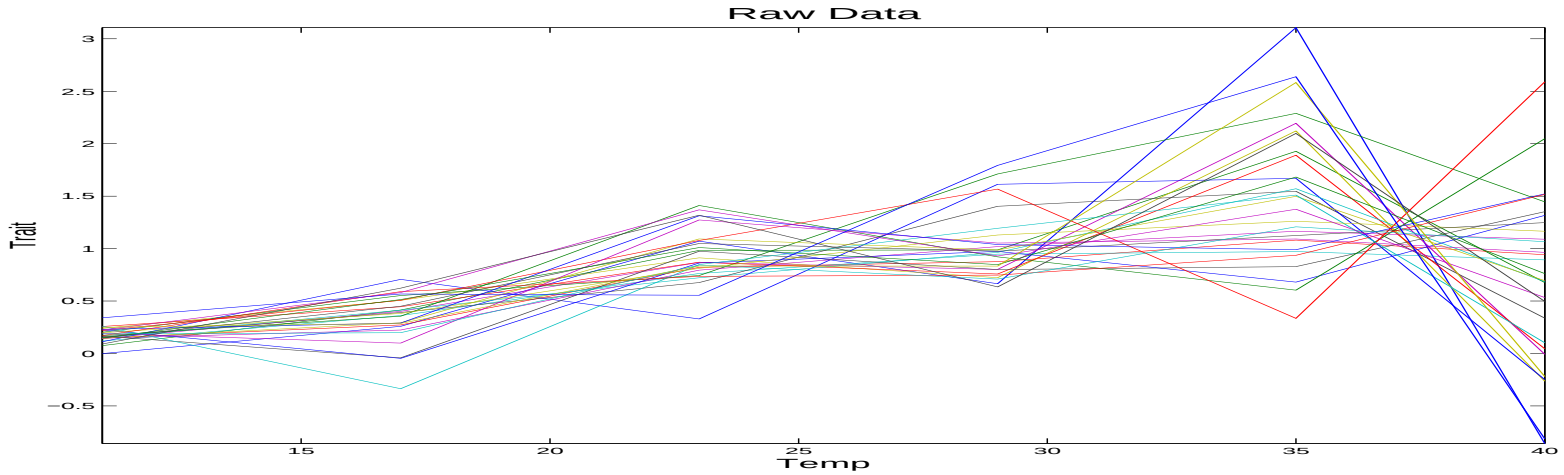
**January 27, 2003**


Raw Data
Trait
Temp
3
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40

Outline

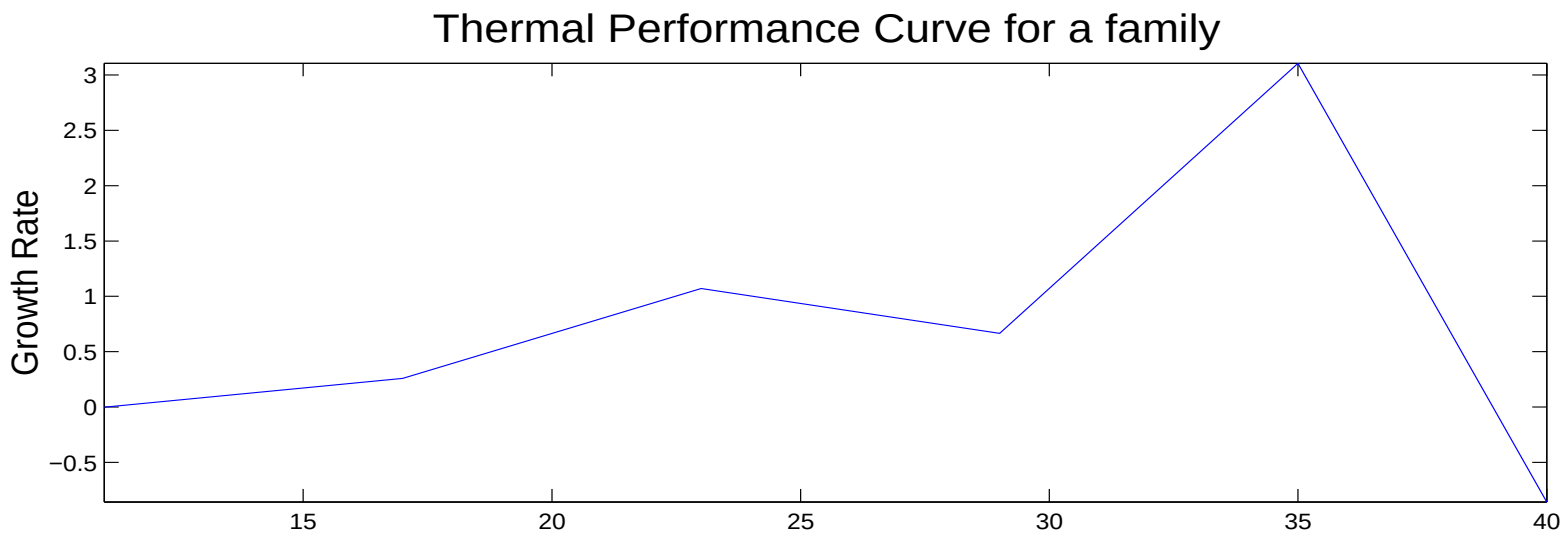
- Data
- Motivation and model
- Toy example
- Results

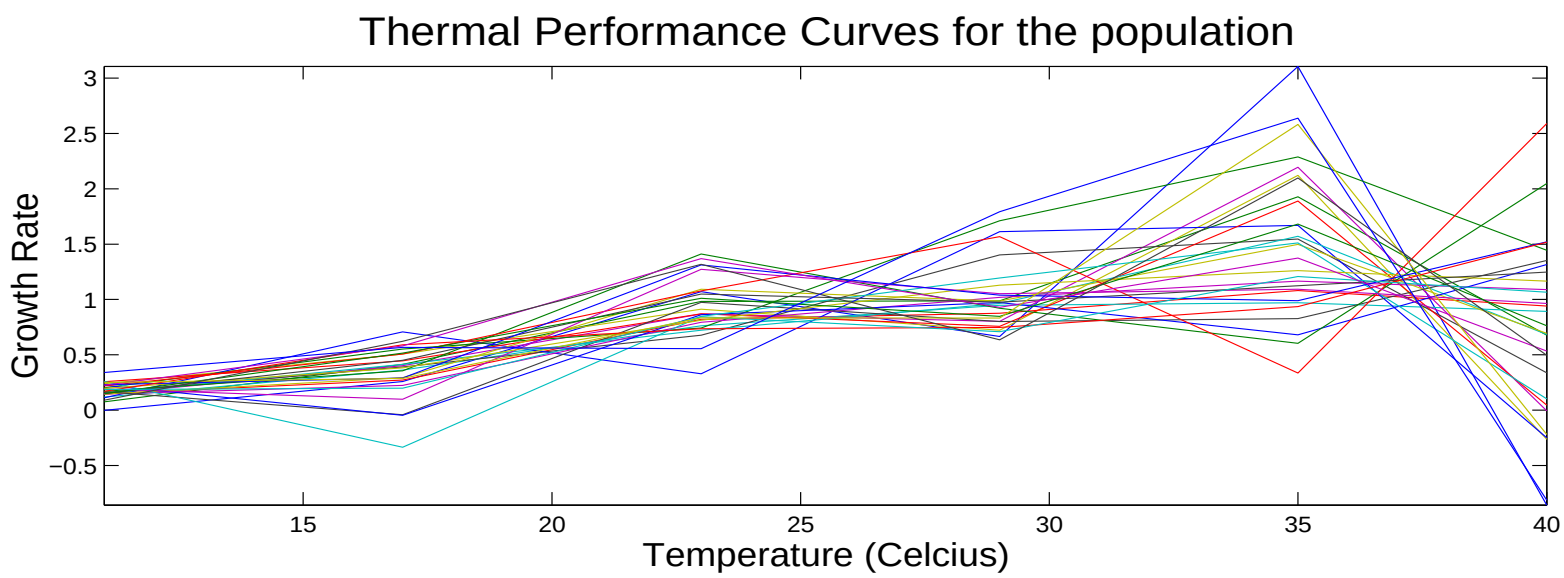
- Performance $z$. Ex: $z =$ growth rate.
- $t$ is the temperature. Ex: $d = 6$, and $t_1, \ldots, t_6 \in [11, 41]$ Celsius.
- Thermal performance curve (TPC): $z = f(t)$.




Template shape $f(t)$ of TPC:

- $\uparrow$, reaches a max and $\downarrow$.
- Rate of $\uparrow$ slower than rate of $\downarrow$.
- Tendency toward a unique max.


Thermal Performance Curve for a family
Growth Rate
3
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40


Thermal Performance Curves for the population
Growth Rate
3
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40
Temperature (Celcius)

- Family $=$ individuals of similar genotype.
  Ex: offsprings of same parents, clones,...
- Population $=$ n families, Ex: $n = 32$.

Outline

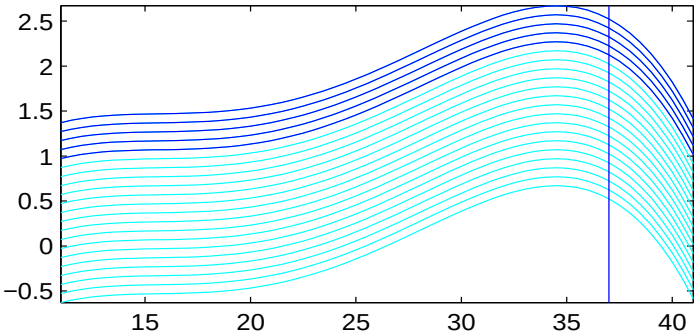
- Data
- Motivation and model
- Toy example
- Results

Variation in TPC = genetic variation in a population

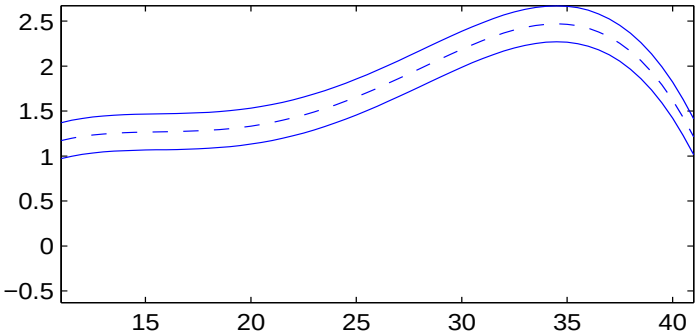
- Goal: quantify three TPC modes of variation.
- Motivation: **evolution** of genetic variation under **selection**.
- Mode of variation ≡ Constraint to evolution

# Mode of variation **before** selection – Genetic variation **after** selection

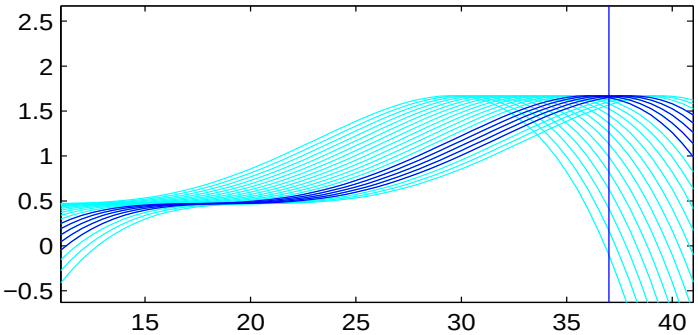
Vertical Shift



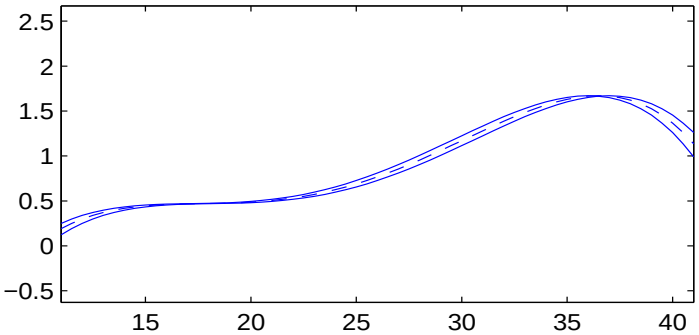

top 25% at t=37



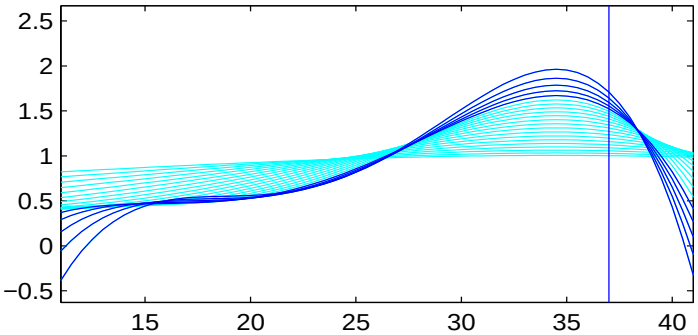

Horizontal Shift



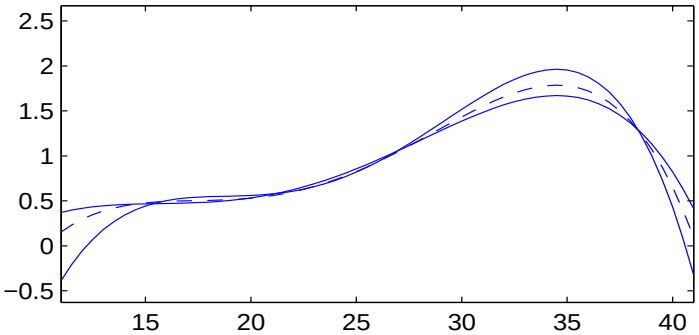

top 25% at t=37




Generalist−Specialist

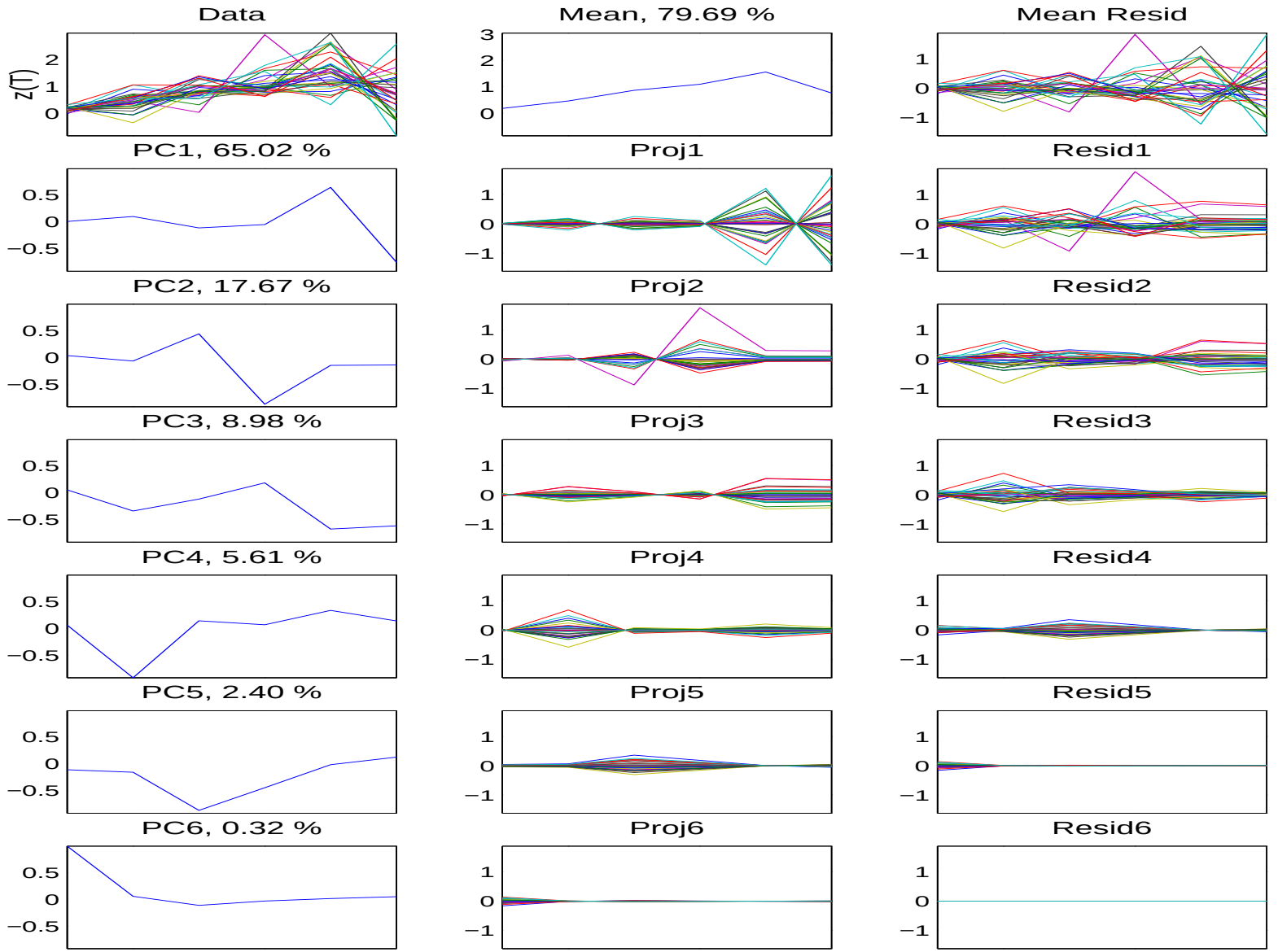



top 25% at t=37

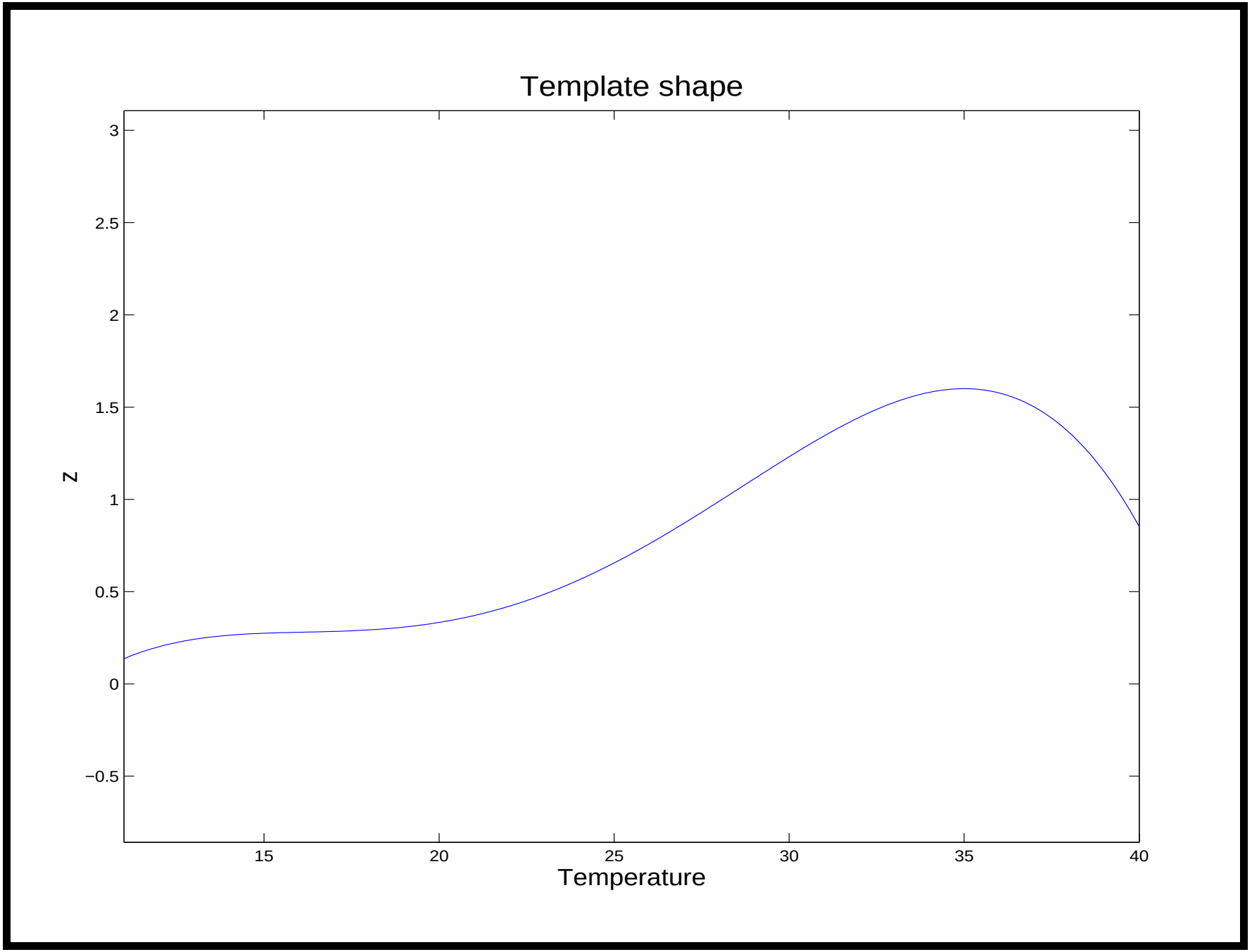


Mode of variation $\equiv$ Constraint to evolution

- Vertical Shift, linear.
- Horizontal Shift, nonlinear.
- Generalist-Specialist, nonlinear.


Data
Mean, 79.69 %
Mean Resid
z(T)
PC1, 65.02 %
Proj1
Resid1
PC2, 17.67 %
Proj2
Resid2
PC3, 8.98 %
Proj3
Resid3
PC4, 5.61 %
Proj4
Resid4
PC5, 2.40 %
Proj5
Resid5
PC6, 0.32 %
Proj6
Resid6

| PCA | Template Modes of Variations |
|---|---|
| No assumption on shape | Template shape of TPCs. |
| **Linear** PC of $G$ | **Nonlinear** modes of variation of $G$. |
| Meaning of each PC? | Biological modes. |
| RSS quantify a PC | $\widetilde{RSS}$ quantify a mode. |


Template shape
3
2.5
2
1.5
1
0.5
0
−0.5
Z
15
20
25
30
35
40
Temperature

Model

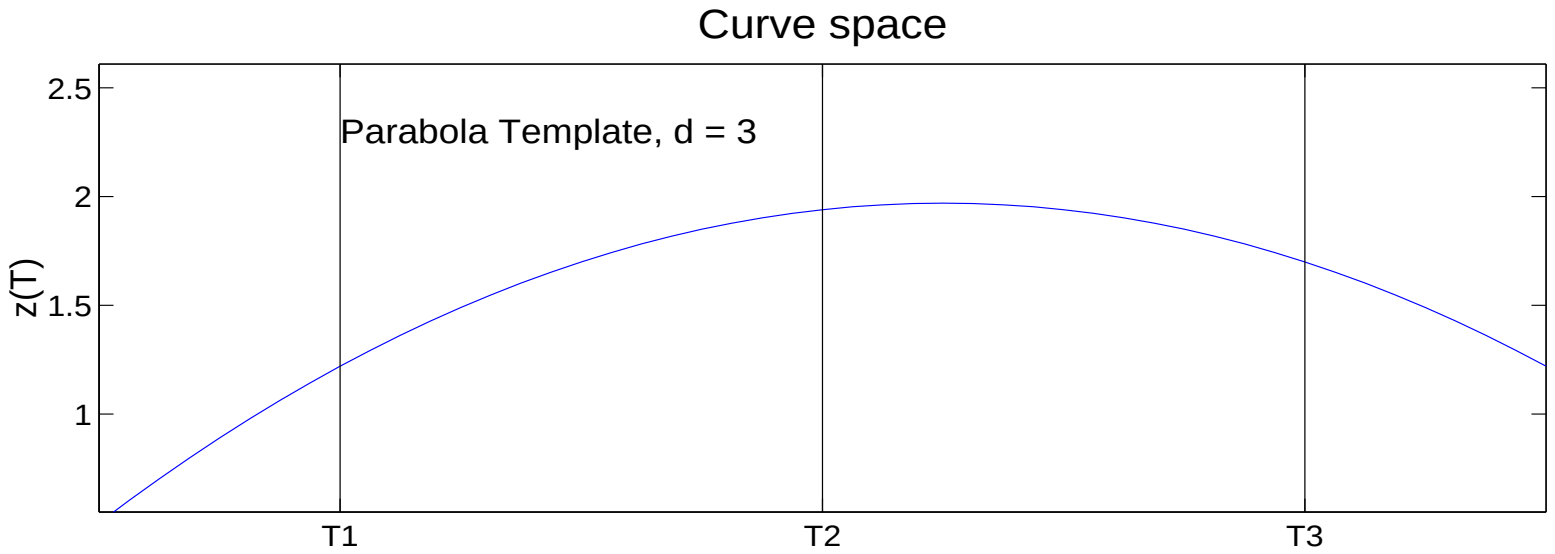
$$Z_i(t_j) = R_i(t_j) + \epsilon_{i,j}, 1 \leq i \leq n \text{ and } 1 \leq j \leq d.$$

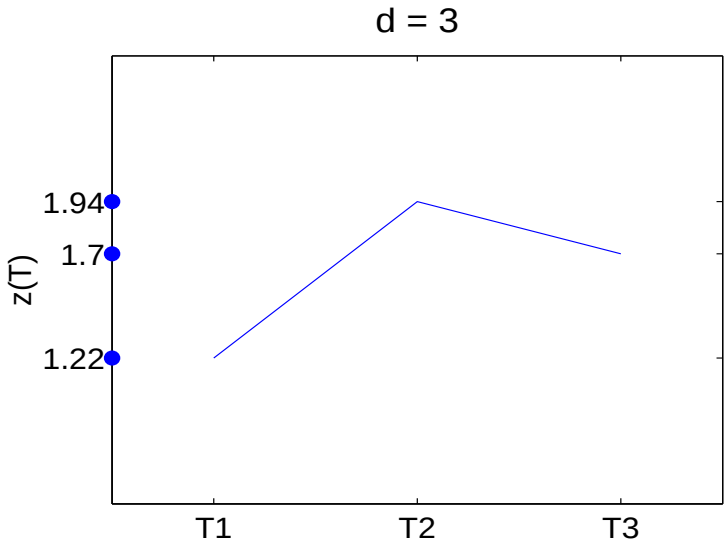
| | $R_i(t)$ | Parameter | Variation |
|---|---|---|---|
| **Vertical shift** | $f(t) + h_i$ | $h_i$ | linear |
| **Horizontal shift** | $f(t - m_i)$ | $m_i$ | nonlinear |
| **Gen-Spec** | $g(w_i)f(w_i t)$, $g(w_i)$ such as $\int_{t_1}^{t_d} R_i(t)dt = C.$ | $w_i$ | nonlinear |

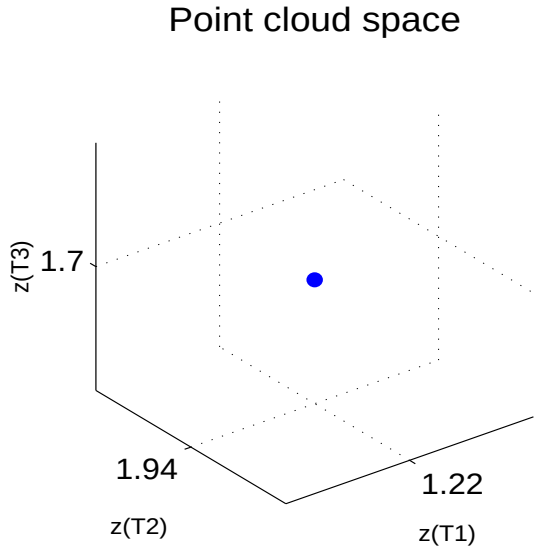
- Parameter of variation is a random variable.
- Linear: parameter space in response space.
- Nonlinear: parameter space is in the temperature space.

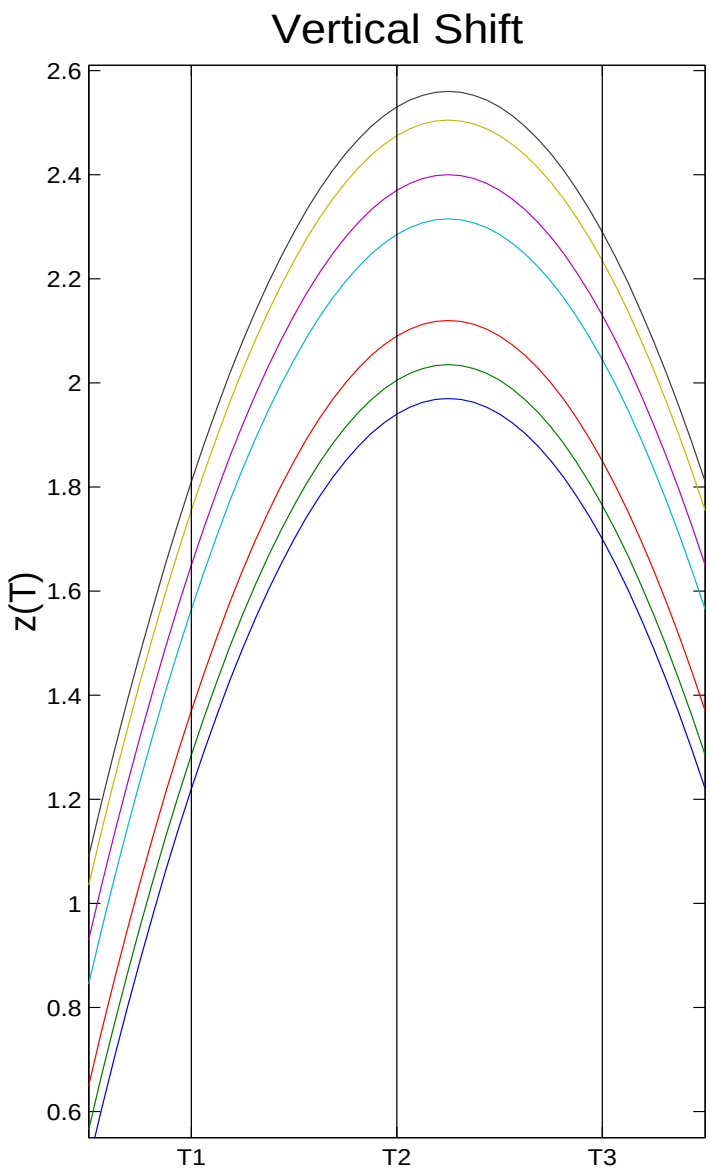
Outline

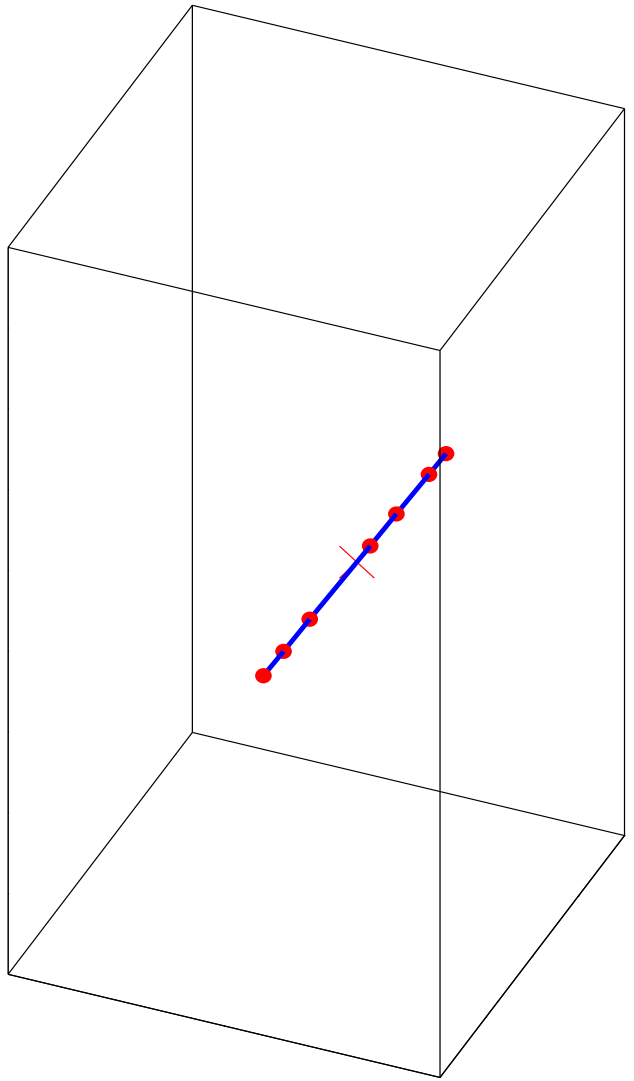
- Data
- Motivation and model
- Toy example
- Results

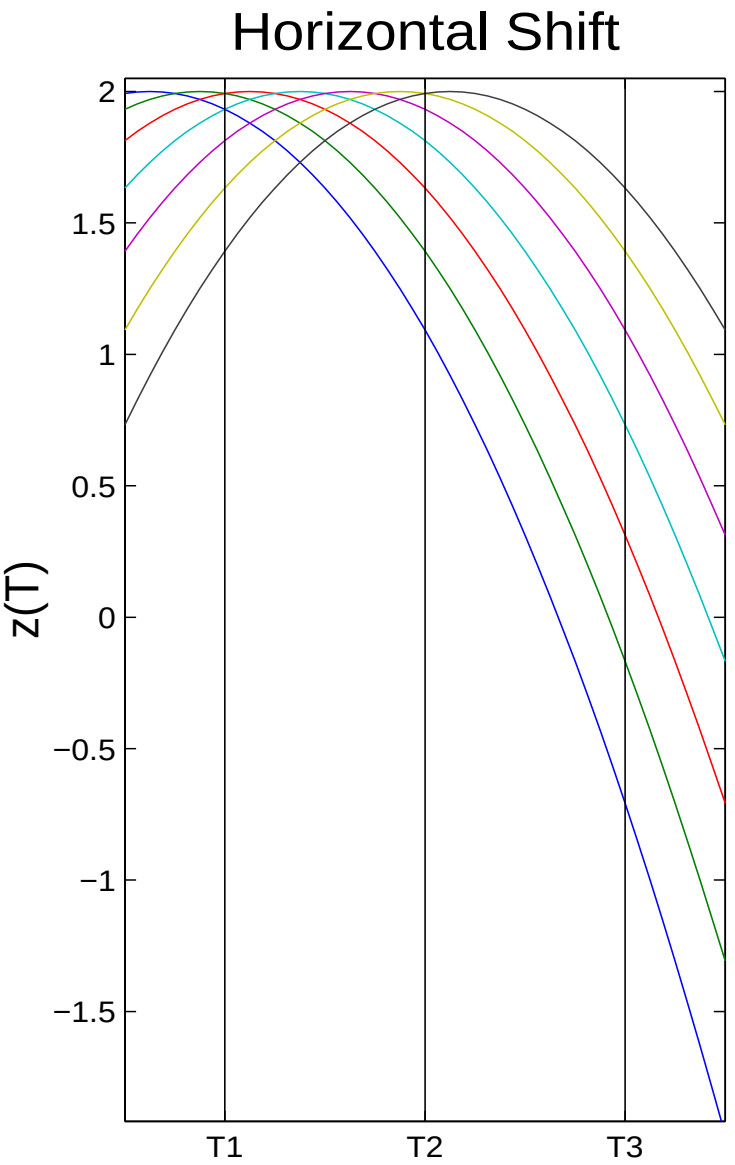

Curve space
Parabola Template, d = 3
z(T)
2.5
2
1.5
1
T1
T2
T3

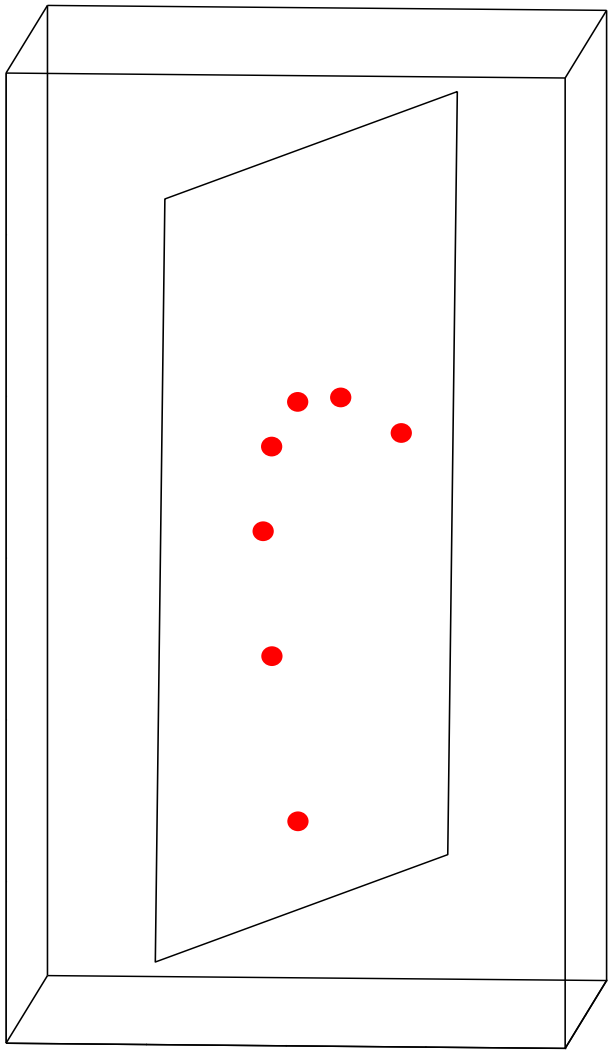

d = 3
z(T)
1.94
1.7
1.22
T1
T2
T3

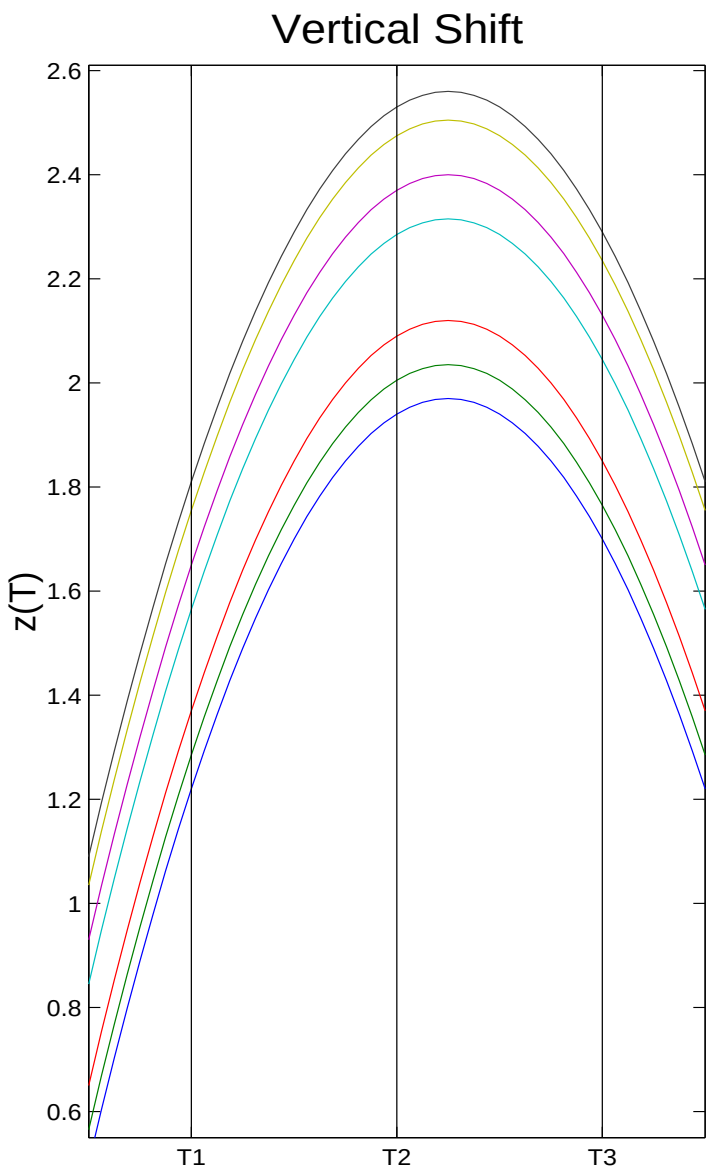

Point cloud space
z(T3)
1.7
1.94
z(T2)
1.22
z(T1)

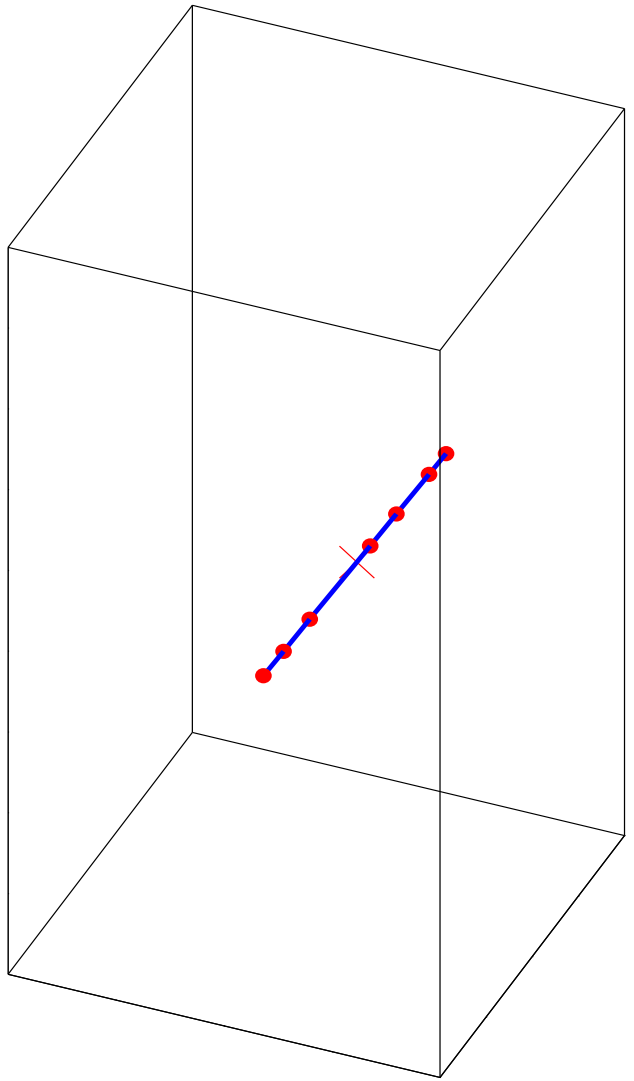

Vertical Shift
z(T)
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
T1
T2
T3




Horizontal Shift
2
1.5
1
0.5
0
−0.5
−1
−1.5
z(T)
T1
T2
T3

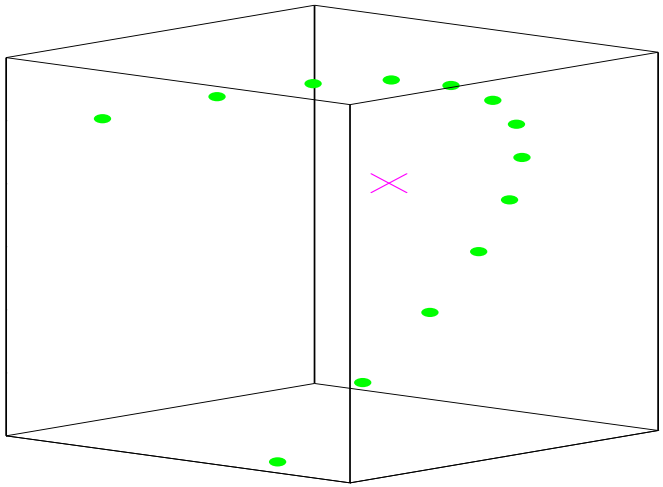


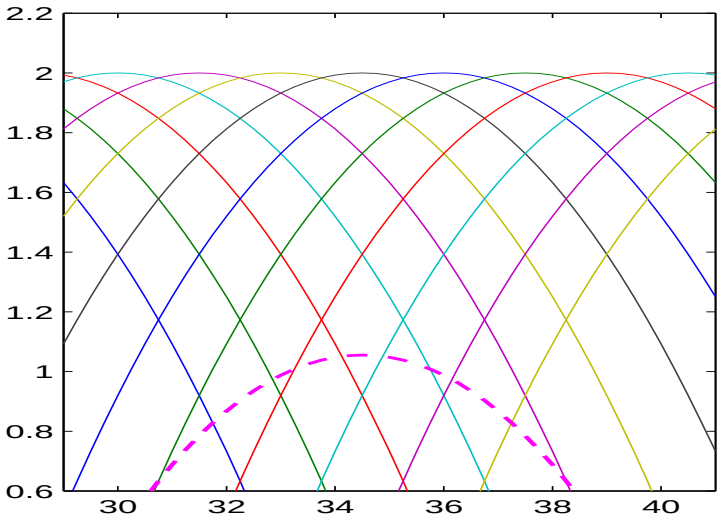

Vertical Shift
z(T)
2.6
2.4
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
T1
T2
T3

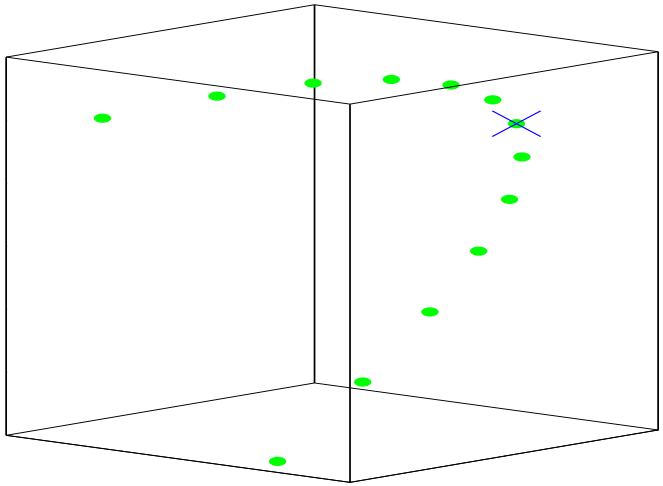


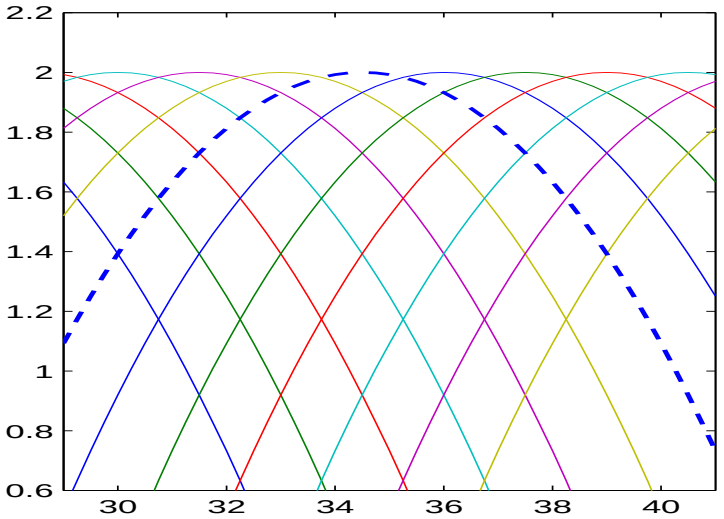
Linear case:

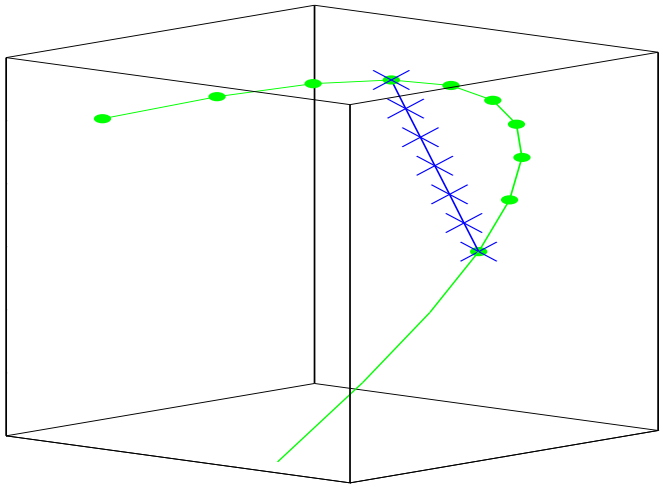
- Center of the projections: $\bar{R}$, and $\bar{R} = \bar{Z}$.
- Spread: $SSM = \sum_{i=1}^{n} ||R_i - \bar{Z}||^2$.
- $RSS = \frac{SSM}{SSM+SSE}$ quantifies the variation.

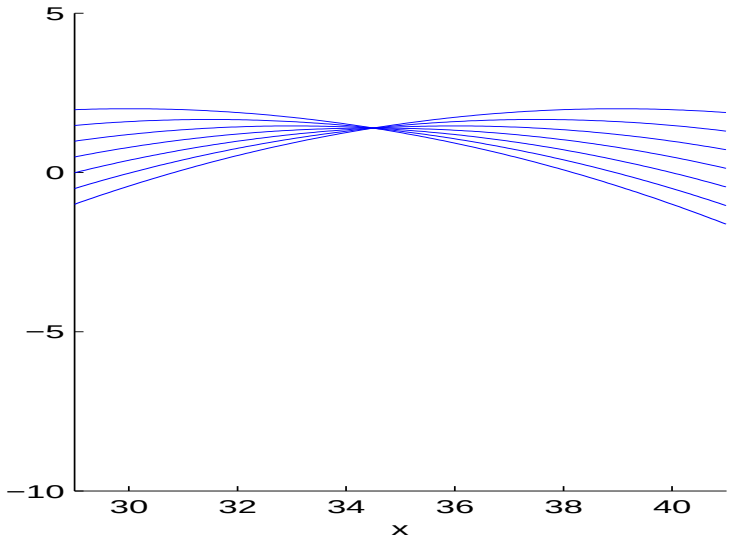


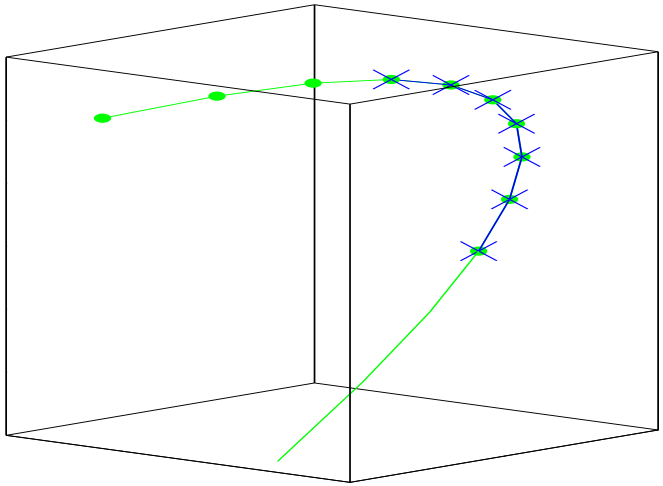

2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
30
32
34
36
38
40

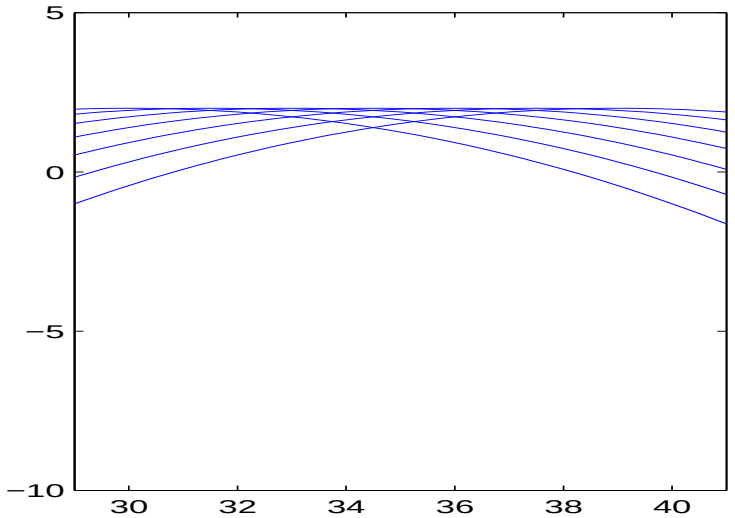



2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
30
32
34
36
38
40




5
0
−5
−10
30
32
34
36
38
40
x




5
0
−5
−10
30
32
34
36
38
40

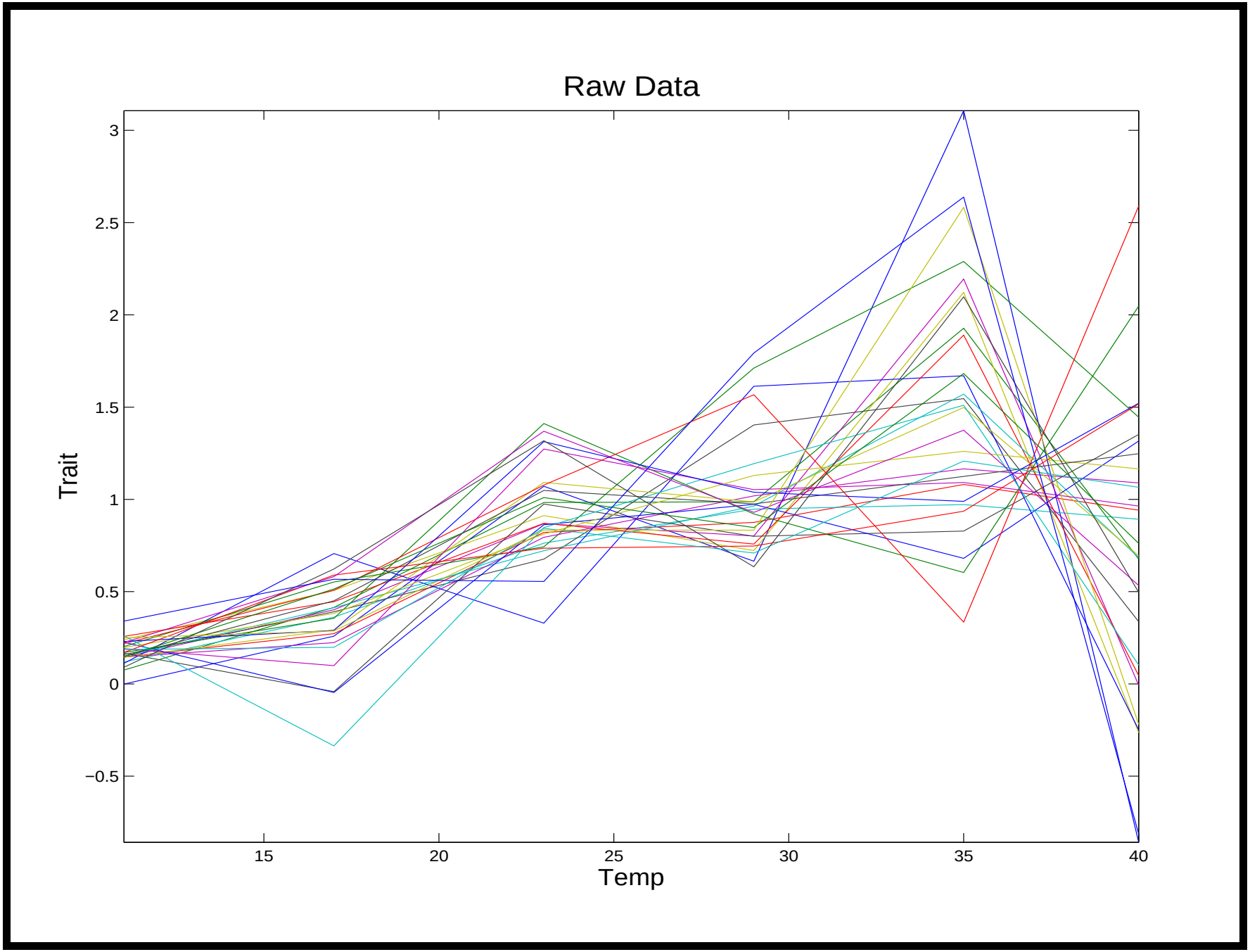
Nonlinear case

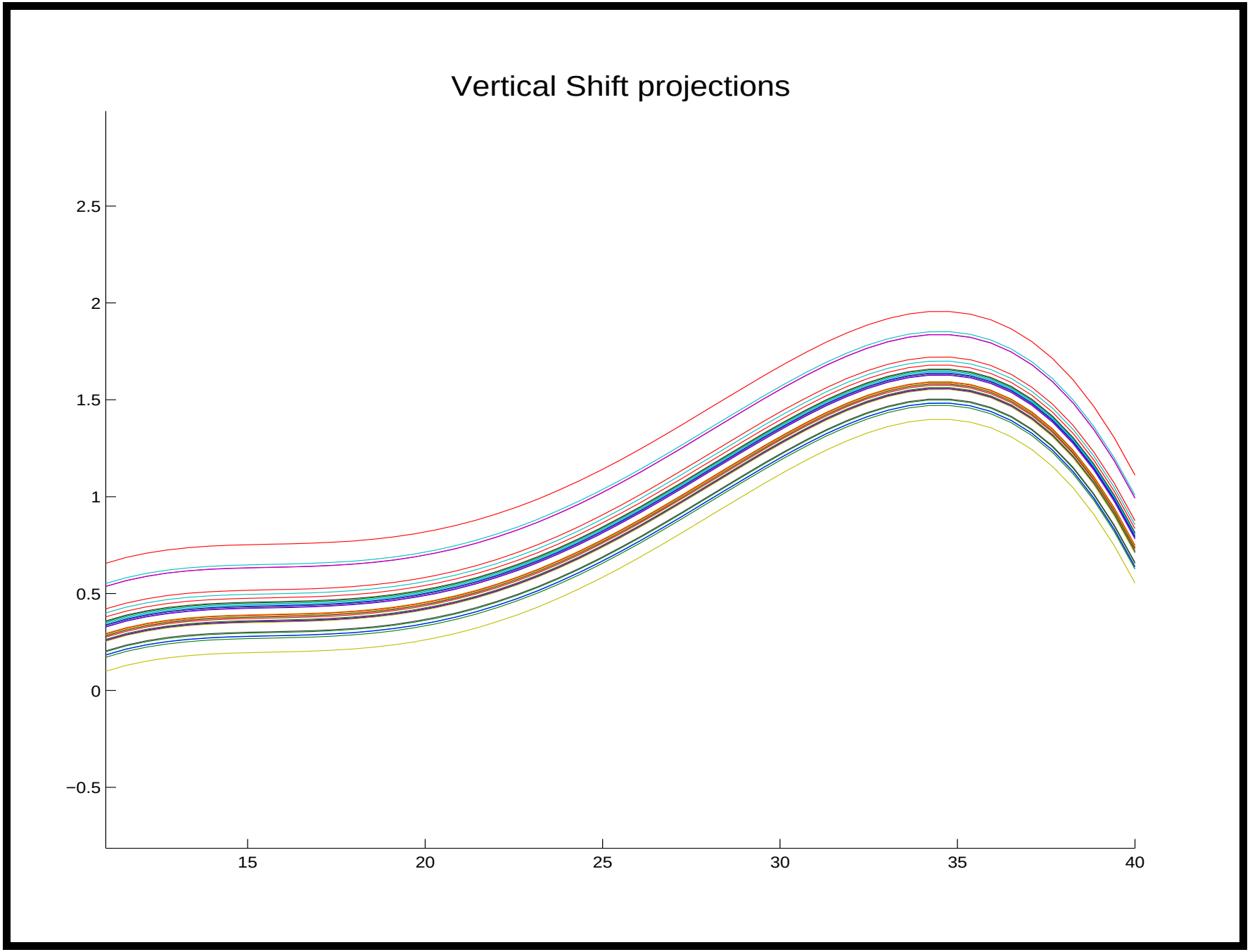
- $\widetilde{R}$ is the sample geodesic mean.
- $d_g$ is the geometric distance.
- $\widetilde{RSS}$ quantifies nonlinear variations.

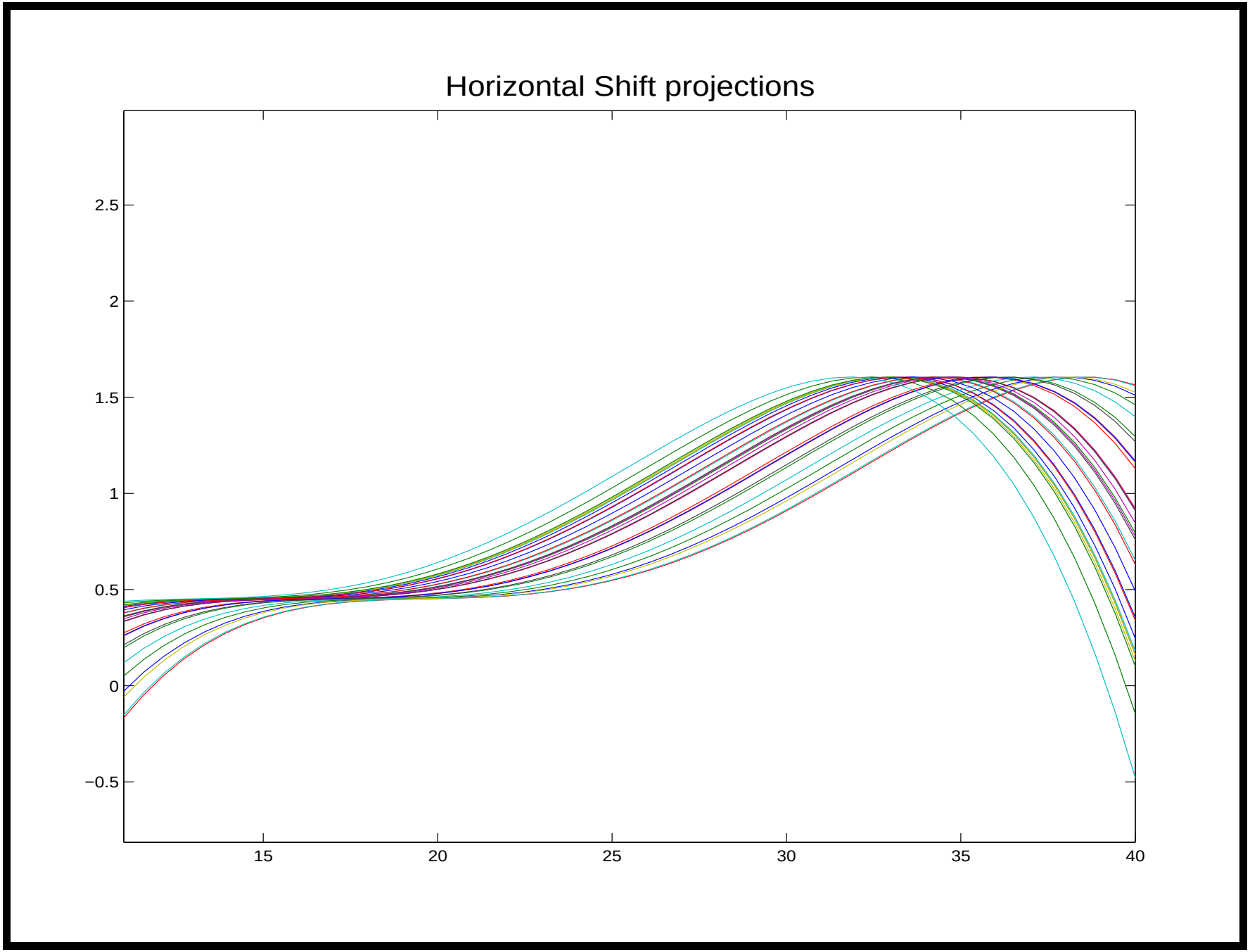
| Linear | Nonlinear |
|---|---|
| $RSS = \frac{SSM}{SSM+SSE}$ | $\widetilde{RSS} = \frac{\widetilde{SSM}}{\widetilde{SSM+SSE}}$ |
| $SSM = \sum_{i=1}^{n} \|\|R_i - \bar{Z}\|\|^2$ | $\widetilde{SSM} = \sum_{i=1}^{n} \left( d_g(R_i, \widetilde{R}) \right)^2$ |
| $\bar{Z} = \bar{R}$ | $\bar{Z} \neq \widetilde{R}$ |
| $SSM \perp SSE$ | $\widetilde{SSM}(\text{not } \perp)SSE$ |

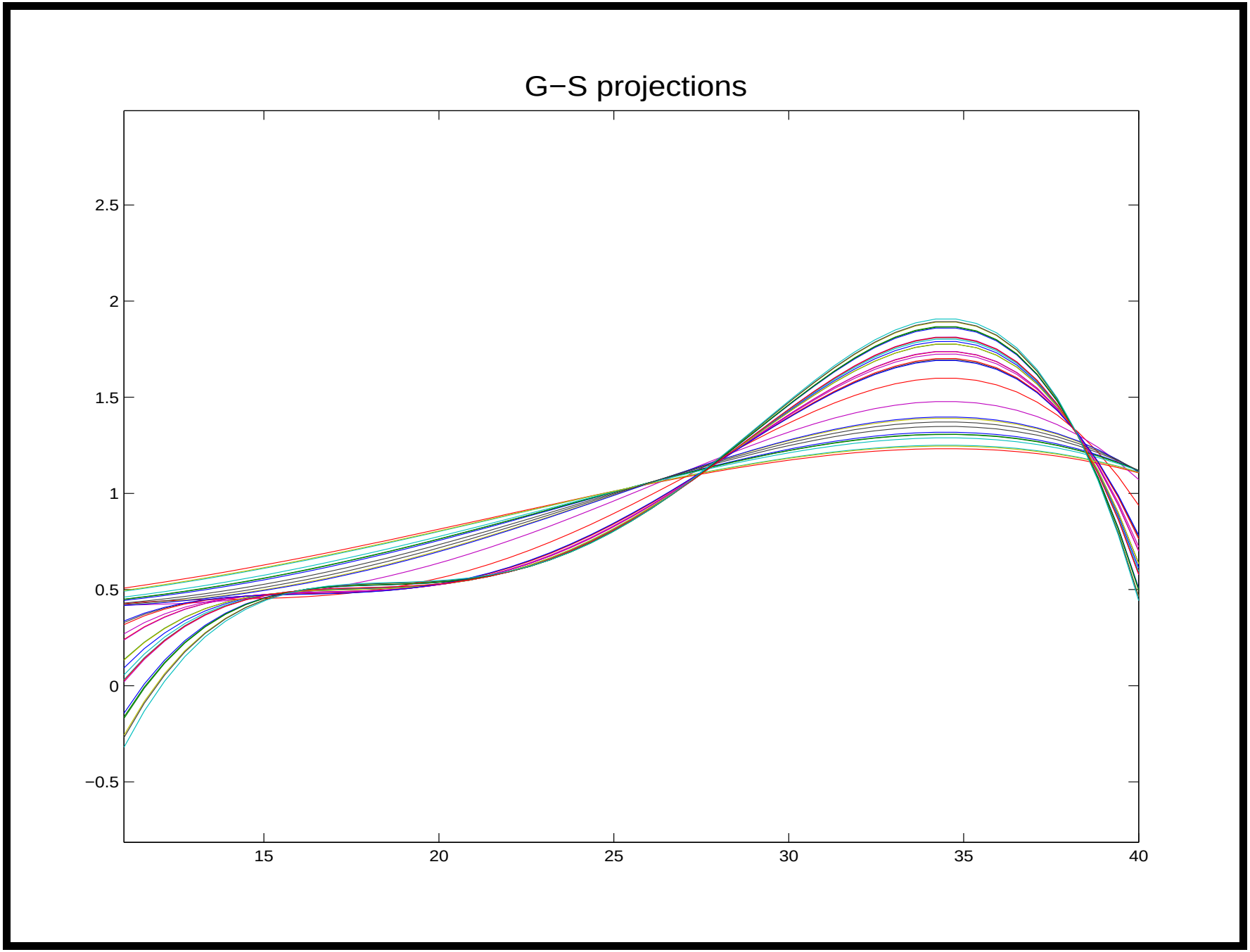
Outline

- Data
- Motivation and model
- Toy example
- Results


Raw Data
Trait
Temp
3
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40


Vertical Shift projections
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40


Horizontal Shift projections
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40


G−S projections
2.5
2
1.5
1
0.5
0
−0.5
15
20
25
30
35
40

| Mode of variation | $SSE$ | $SSM(RSS)$ | $\widetilde{SSM}(\widetilde{RSS})$ |
|---|---|---|---|
| Vertical Shift | $42.67$ | $2.69(6\%)$ | $2.69(6\%)$ |
| Horizontal Shift | $32.44$ | $12.11(27\%)$ | $13.36(29\%)$ |
| Generalist Specialist | $31.97$ | $6.63(17\%)$ | $9.71(23.30\%)$ |

Conclusion in evolutionary biology: Selecting for higher growth rate in a range of temperature will not result in higher growth rate at all temperatures.

Family parameters

| Mode of variation | Parameter | range (mean,sd) |
|---|---|---|
| Vertical Shift | $h_i$ | $[1.38, 1.96](1.62, 0.12)$ |
| Horizontal Shift | $m_i$ | $[31.85, 38.59](34.9, 1.88)$ |
| Generalist-Specialist | $w_i$ | $[0.49, 1.19](0.92, 0.26)$ |

Summary: One variation at a time

- Parameters optimized to minimize the $SSE$.
- Variation of parameter $\Rightarrow$ Variation of data.
- $\widetilde{RSS}$ was measured by discrete approximation.

- The modes of variations overlap each other.
- $\widetilde{SSM}$ not orthogonal to $SEE$.

Work in progress: Simultaneous variation $g(w_i)f(w_i(t-m_i))+h_i$

- Projection on each mode.
- Quantification of each variation.
- Decomposition of the total variation in the three modes.