# A Genetic Signature of Host-Parasite Coevolution in Continuous Space

A Preprint

**Bob Week**
Integrative Biology
Michigan State University
East Lansing, MI 48824
weekrobe@msu.edu

**Gideon Bradburd**
Integrative Biology
Michigan State University
East Lansing, MI 48824
bradburd@msu.edu

January 27, 2021

## Abstract

Here we identify a genetic signature of host-parasite coevolution in continuous space using spatial patterns of linkage-disequilibrium.

***K*eywords** blah · blee · bloo · these are optional and can be removed

## 1 Introduction

We consider a biallelic haploid two-locus model of fitness for each species. For the host and parasite we denote the possible haplotypes respectively by $p^H_{AB}, p^H_{Ab}, p^H_{aB}, p^H_{ab}$ and $p^P_{AB}, p^P_{Ab}, p^P_{aB}, p^P_{ab}$. Similarly, gene frequencies are denoted by $p^X_A$ and $p^X_B$ for species $X = H, P$. Linkage disequilibrium within species $X$ can be written as $D_X = p^X_{AB} - p^X_A p^X_B$ or $D_X = p^X_{AB} p^X_{ab} - p^X_{Ab} p^X_{aB}$. We assume that individuals encounter each at random and that when a host individual with haploid genotype $i$ encounters a parasite individual with haploid genotype $i$, infection occurs with probability $\alpha_{ij}$. Given an infection occurs, we assume the host experiences a reduction in fitness by the amount $s_H$. Hence, per-capita growth rates of host haplotypes are given by

$$m^H_{AB} = -s_H(\alpha_{AB,AB}p^P_{AB} + \alpha_{AB,Ab}p^P_{Ab} + \alpha_{AB,aB}p^P_{aB} + \alpha_{AB,ab}p^P_{ab}), \tag{1a}$$

$$m^H_{aB} = -s_H(\alpha_{aB,AB}p^P_{AB} + \alpha_{aB,Ab}p^P_{Ab} + \alpha_{aB,aB}p^P_{aB} + \alpha_{aB,ab}p^P_{ab}), \tag{1b}$$

$$m^H_{Ab} = -s_H(\alpha_{Ab,AB}p^P_{AB} + \alpha_{Ab,Ab}p^P_{Ab} + \alpha_{Ab,aB}p^P_{aB} + \alpha_{Ab,ab}p^P_{ab}), \tag{1c}$$

$$m^H_{ab} = -s_H(\alpha_{ab,AB}p^P_{AB} + \alpha_{ab,Ab}p^P_{Ab} + \alpha_{ab,aB}p^P_{aB} + \alpha_{ab,ab}p^P_{ab}). \tag{1d}$$

Similarly, by assuming infection increases per-capita growth rates of parasite haplotypes by the amount $s_P$, we obtain

$$m^P_{AB} = -s_H(\alpha_{AB,AB}p^H_{AB} + \alpha_{Ab,AB}p^H_{Ab} + \alpha_{aB,AB}p^H_{aB} + \alpha_{ab,AB}p^H_{ab}), \tag{2a}$$

$$m^P_{AB} = -s_H(\alpha_{AB,aB}p^H_{AB} + \alpha_{Ab,aB}p^H_{Ab} + \alpha_{aB,aB}p^H_{aB} + \alpha_{ab,aB}p^H_{ab}), \tag{2b}$$

$$m^P_{Ab} = -s_H(\alpha_{AB,Ab}p^H_{AB} + \alpha_{Ab,Ab}p^H_{Ab} + \alpha_{aB,Ab}p^H_{aB} + \alpha_{ab,Ab}p^H_{ab}), \tag{2c}$$

$$m^P_{ab} = -s_H(\alpha_{AB,ab}p^H_{AB} + \alpha_{Ab,ab}p^H_{Ab} + \alpha_{aB,ab}p^H_{aB} + \alpha_{ab,ab}p^H_{ab}). \tag{2d}$$

The per-capita population growth rate of species $X$ can then be written as $\bar{m}_X = m^X_{AB}p^X_{AB} + m^X_{aB}p^X_{aB} + m^X_{Ab}p^X_{Ab} + m^X_{ab}p^X_{ab}$. Assuming clonal reproduction, we can write down the evolution of haploid genotype frequency $p^X_i$ as

$$\frac{dp^X_i}{dt} = (m^X_i - \bar{m}_X)p^X_i. \tag{3}$$

However, since our interests are in sexually reproducing diploid organisms we need to extend this model.

## 2 Headings: first level

Quisque ullamcorper placerat ipsum. Cras nibh. Morbi vel justo vitae lacus tincidunt ultrices. Lorem ipsum dolor sit amet, consectetuer adipiscing elit. In hac habitasse platea dictumst. Integer tempus convallis augue. Etiam facilisis. Nunc elementum fermentum wisi. Aenean placerat. Ut imperdiet, enim sed gravida sollicitudin, felis odio placerat quam, ac pulvinar elit purus eget enim. Nunc vitae tortor. Proin tempus nibh sit amet nisl. Vivamus quis tortor vitae risus porta vehicula. See Section 2.

### 2.1 Headings: second level

Fusce mauris. Vestibulum luctus nibh at lectus. Sed bibendum, nulla a faucibus semper, leo velit ultricies tellus, ac venenatis arcu wisi vel nisl. Vestibulum diam. Aliquam pellentesque, augue quis sagittis posuere, turpis lacus congue quam, in hendrerit risus eros eget felis. Maecenas eget erat in sapien mattis porttitor. Vestibulum porttitor. Nulla facilisi. Sed a turpis eu lacus commodo facilisis. Morbi fringilla, wisi in dignissim interdum, justo lectus sagittis dui, et vehicula libero dui cursus dui. Mauris tempor ligula sed lacus. Duis cursus enim ut augue. Cras ac magna. Cras nulla. Nulla egestas. Curabitur a leo. Quisque egestas wisi eget nunc. Nam feugiat lacus vel est. Curabitur consectetuer.

$$\xi_{ij}(t) = P(x_t = i, x_{t+1} = j|y, v, w; \theta) = \frac{\alpha_i(t)a^{w_t}_{ij}\beta_j(t+1)b^{v_{t+1}}_j(y_{t+1})}{\sum_{i=1}^N \sum_{j=1}^N \alpha_i(t)a^{w_t}_{ij}\beta_j(t+1)b^{v_{t+1}}_j(y_{t+1})}$$

#### 2.1.1 Headings: third level

Suspendisse vel felis. Ut lorem lorem, interdum eu, tincidunt sit amet, laoreet vitae, arcu. Aenean faucibus pede eu ante. Praesent enim elit, rutrum at, molestie non, nonummy vel, nisl. Ut lectus eros, malesuada sit amet, fermentum eu, sodales cursus, magna. Donec eu purus. Quisque vehicula, urna sed ultricies auctor, pede lorem egestas dui, et convallis elit erat sed nulla. Donec luctus. Curabitur et nunc. Aliquam dolor odio, commodo pretium, ultricies non, pharetra in, velit. Integer arcu est, nonummy in, fermentum faucibus, egestas vel, odio.

**Paragraph** Sed commodo posuere pede. Mauris ut est. Ut quis purus. Sed ac odio. Sed vehicula hendrerit sem. Duis non odio. Morbi ut dui. Sed accumsan risus eget odio. In hac habitasse platea dictumst. Pellentesque non elit. Fusce sed justo eu urna porta tincidunt. Mauris felis odio, sollicitudin sed, volutpat a, ornare ac, erat. Morbi quis dolor. Donec pellentesque, erat ac sagittis semper, nunc dui lobortis purus, quis congue purus metus ultricies tellus. Proin et quam. Class aptent taciti sociosqu ad litora torquent per conubia nostra, per inceptos hymenaeos. Praesent sapien turpis, fermentum vel, eleifend faucibus, vehicula eu, lacus.

## 3 Examples of citations, figures, tables, references

Pellentesque habitant morbi tristique senectus et netus et malesuada fames ac turpis egestas. Donec odio elit, dictum in, hendrerit sit amet, egestas sed, leo. Praesent feugiat sapien aliquet odio. Integer vitae justo. Aliquam vestibulum fringilla lorem. Sed neque lectus, consectetuer at, consectetuer sed, eleifend ac, lectus. Nulla facilisi. Pellentesque eget lectus. Proin eu metus. Sed porttitor. In hac habitasse platea dictumst. Suspendisse eu lectus. Ut mi mi, lacinia sit amet, placerat et, mollis vitae, dui. Sed ante tellus, tristique ut, iaculis eu, malesuada ac, dui. Mauris nibh leo, facilisis non, adipiscing quis, ultrices a, dui. some text (Kour and Saabne 2014b, 2014a) and see Hadash et al. (2018).

The documentation for `natbib` may be found at

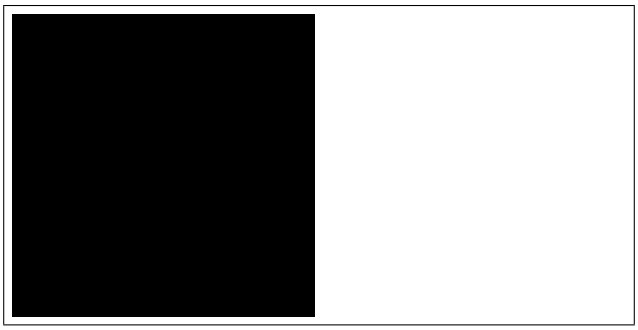


Figure 1: Sample figure caption.

`http://mirrors.ctan.org/macros/latex/contrib/natbib/natnotes.pdf`

Of note is the command `\citet`, which produces citations appropriate for use in inline text. For example,

```
\citet{hasselmo} investigated\dots
```

produces

> Hasselmo, et al. (1995) investigated...

`https://www.ctan.org/pkg/booktabs`

### 3.1 Figures

Suspendisse vitae elit. Aliquam arcu neque, ornare in, ullamcorper quis, commodo eu, libero. Fusce sagittis erat at erat tristique mollis. Maecenas sapien libero, molestie et, lobortis in, sodales eget, dui. Morbi ultrices rutrum lorem. Nam elementum ullamcorper leo. Morbi dui. Aliquam sagittis. Nunc placerat. Pellentesque tristique sodales est. Maecenas imperdiet lacinia velit. Cras non urna. Morbi eros pede, suscipit ac, varius vel, egestas non, eros. Praesent malesuada, diam id pretium elementum, eros sem dictum tortor, vel consectetuer odio sem sed wisi.

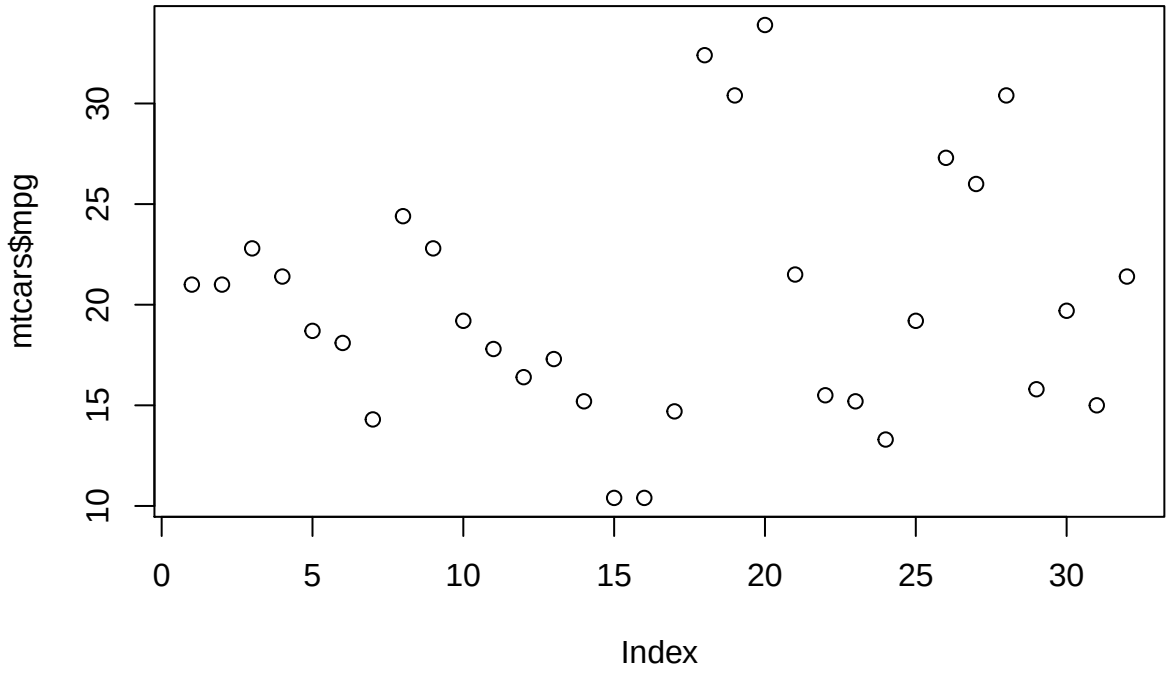
See Figure 1. Here is how you add footnotes. [^Sample of the first footnote.]

Sed feugiat. Cum sociis natoque penatibus et magnis dis parturient montes, nascetur ridiculus mus. Ut pellentesque augue sed urna. Vestibulum diam eros, fringilla et, consectetuer eu, nonummy id, sapien. Nullam at lectus. In sagittis ultrices mauris. Curabitur malesuada erat sit amet massa. Fusce blandit. Aliquam erat volutpat. Aliquam euismod. Aenean vel lectus. Nunc imperdiet justo nec dolor.

```r
plot(mtcars$mpg)
```

Table 1: Sample table title

| Part | | |
|---|---|---|
| Name | Description | Size ($\mu$m) |
| Dendrite | Input terminal | $\sim$100 |
| Axon | Output terminal | $\sim$10 |
| Soma | Cell body | up to $10^6$ |




### 3.2 Tables

Etiam euismod. Fusce facilisis lacinia dui. Suspendisse potenti. In mi erat, cursus id, nonummy sed, ullamcorper eget, sapien. Praesent pretium, magna in eleifend egestas, pede pede pretium lorem, quis consectetuer tortor sapien facilisis magna. Mauris quis magna varius nulla scelerisque imperdiet. Aliquam non quam. Aliquam porttitor quam a lacus. Praesent vel arcu ut tortor cursus volutpat. In vitae pede quis diam bibendum placerat. Fusce elementum convallis neque. Sed dolor orci, scelerisque ac, dapibus nec, ultricies ut, mi. Duis nec dui quis leo sagittis commodo.

See awesome Table~1.

### 3.3 Lists

- Lorem ipsum dolor sit amet
- consectetur adipiscing elit.
- Aliquam dignissim blandit est, in dictum tortor gravida eget. In ac rutrum magna.

Hadash, Guy, Einat Kermany, Boaz Carmeli, Ofer Lavi, George Kour, and Alon Jacovi. 2018. "Estimate and Replace: A Novel Approach to Integrating Deep Neural Networks with Existing Applications." *arXiv Preprint arXiv:1804.09028*.

Kour, George, and Raid Saabne. 2014a. "Fast Classification of Handwritten on-Line Arabic Characters." In *Soft Computing and Pattern Recognition (Socpar), 2014 6th International Conference of*, 312–18. IEEE.

———. 2014b. "Real-Time Segmentation of on-Line Handwritten Arabic Script." In *Frontiers in Handwriting Recognition (Icfhr), 2014 14th International Conference on*, 417–22. IEEE.