Meta-analysis of the parasitism levels of Harmonia axyridis

Gilles San Martin

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Contents

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1 Introduction - context

Data from the review paper :

Ceryngier et al. (submitted in 2017) Predators and parasitoids of the harlequin ladybird, Harmonia axyridis, in its native range and invaded areas. Biological Invasions

This analysis was performed by Gilles San Martin with inputs from other authors of the review, mainly Piotr Ceryngier and Danny Haelewaters. The full analysis, R code and raw data are available from the following public figshare repository : https://figshare.com/s/5d1a0d38be7d0941a455

We analysed only the parasitoïd data from tables 3 and 4 of the paper. For *Dinocampus coccinellae*, we used both parasitism rates determined by dissection of field collected ladybirds and emergence level of the parasitoïds (in separate analyses) and for *Phalacrotophora spp.* we used only the parasitism level ascertained as the proportion of field collected ladybirds pupae giving rise to the parasitoïd larvae. For these three dataset, we checked if we could find differences between regions, between species and if we could find temporal trends.

These data are mainly data gathered from the literature, with different protocols, scope, etc and all the problems that can occur with this kind of data.
For the parasitism/emergence rate data we generally have only one rounded percentage value and the total number of observations. As the rounded % is not an exact ratio of two integers this causes some warnings when used in binomial GLMs. However this should be a minor concern. For the Phalacrotophora data we have artificialy fixed the total number of observations to a conservative value when it was not available in the literature (see chapter 4 for more details).

2 *Dinocampus coccinellae* parasitism rate

Summary of the data :

```
##                           Localisation          Country
##  Bologna area, Italy          : 6   Chile         : 6
##  Santiago, Chile              : 6   Italy         : 6
##  West Cape Province, South Africa: 5   USA         : 6
##  Minnesota, USA               : 4   South Africa  : 5
##  the Netherlands              : 3   United Kingdom: 5
##  UK                           : 3   Japan         : 3
##  (Other)                      :14   (Other)       :10
##         Continent          Range      Year_start        Year
##  Africa        : 5  Invaded area:38  Min.   :1993  Min.   :1960
##  Asia          : 3  Native range: 3  1st Qu.:2001  1st Qu.:2002
##  Europe        :19                   Median :2006  Median :2010
##  North America: 8                    Mean   :2004  Mean   :2006
##  South America: 6                    3rd Qu.:2009  3rd Qu.:2013
##                                      Max.   :2011  Max.   :2016
##                                      NA's   :37
##                        Host    Parasitism_rate  Parasitism_N
##  Harmonia axyridis        :24   Min.   : 0.00   Min.   :  14.0
##  Coccinella septempunctata: 4   1st Qu.: 1.20   1st Qu.: 101.0
##  Hippodamia variegata     : 4   Median : 8.90   Median : 237.0
##  Coleomegilla maculata    : 3   Mean   :13.03   Mean   : 368.1
##  Eriopis chilensis        : 2   3rd Qu.:23.80   3rd Qu.: 453.0
##  Adalia bipunctata        : 1   Max.   :46.40   Max.   :1652.0
##  (Other)                  : 3   NA's   :20      NA's   :20
##  Emergence_rate    Emergence_N                              Reference
##  Min.   : 0.000   Min.   :    35   A. Grez and T. Zaviezo., unpubl.: 6
##  1st Qu.: 0.500   1st Qu.:    57   Minnaar et al. 2014             : 5
##  Median : 3.450   Median :   125   Dindo et al. 2016               : 4
##  Mean   : 5.483   Mean   :  1025   Hoogendoorn & Heimpel 2002      : 4
##  3rd Qu.: 8.300   3rd Qu.:   474   Maeta 1969b                     : 3
##  Max.   :26.100   Max.   :18952    Raak-van den Berg et al. 2014   : 3
##  NA's   :11       NA's   :12       (Other)                         :16
```
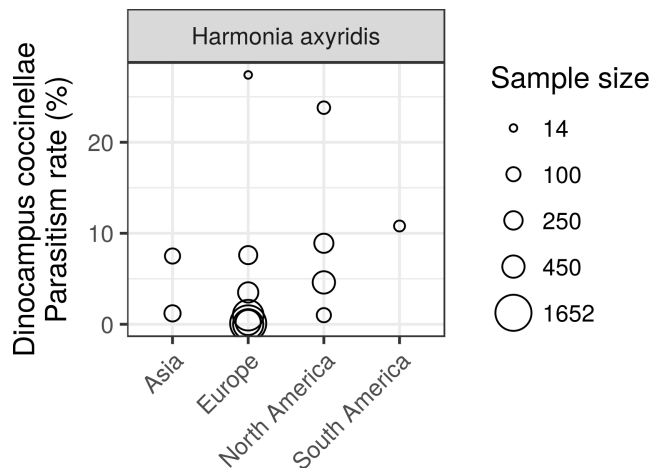
2.1 Comparing parasitism rates between regions

2.1.1 Graph

Figure 1:

2.1.2 GLM

Is the parasitism rate of H. axyridis different between regions (continents) ?

We performed a Binomial GLM with a quasilikelihood approach to estimate the overdispersion coefficient (that is quite high here : ~ 31).
There is no statistically significant difference between the regions (quasibinomial GLM, $F_{3,10} = 3.66$, p = 0.35)
NB : we use a specific F test adapted to overdispersed GLMs instead of the more classical Likelihood Ratio Test

Table 1: Analysis of Deviance Table (Type II tests)

	SS	Df	F	Pr(>F)
Continent	114.4	3	1.22	0.3526
Residuals	312.6	10	NA	NA

```
## 
## Call:
## glm(formula = Parasitism_rate/100 ~ Continent, family = quasibinomial,
##     data = tmp, weights = Parasitism_N)
## 
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -4.5501  -2.3004   0.0877   3.2566   6.6739
## 
## Coefficients:
##                       Estimate Std. Error t value Pr(>|t|)
## (Intercept)            -3.1849     1.6720  -1.905   0.0859 .
## ContinentEurope        -1.4642     1.8602  -0.787   0.4495
## ContinentNorth America  0.5812     1.8269   0.318   0.7569
## ContinentSouth America  1.0736     3.4007   0.316   0.7587
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
## 
## (Dispersion parameter for quasibinomial family taken to be 31.25669)
## 
##     Null deviance: 278.61  on 13  degrees of freedom
## Residual deviance: 164.21  on 10  degrees of freedom
## AIC: NA
## 
## Number of Fisher Scoring iterations: 6
```

2.2   Comparing parasitism rate between species

2.2.1   Graphs

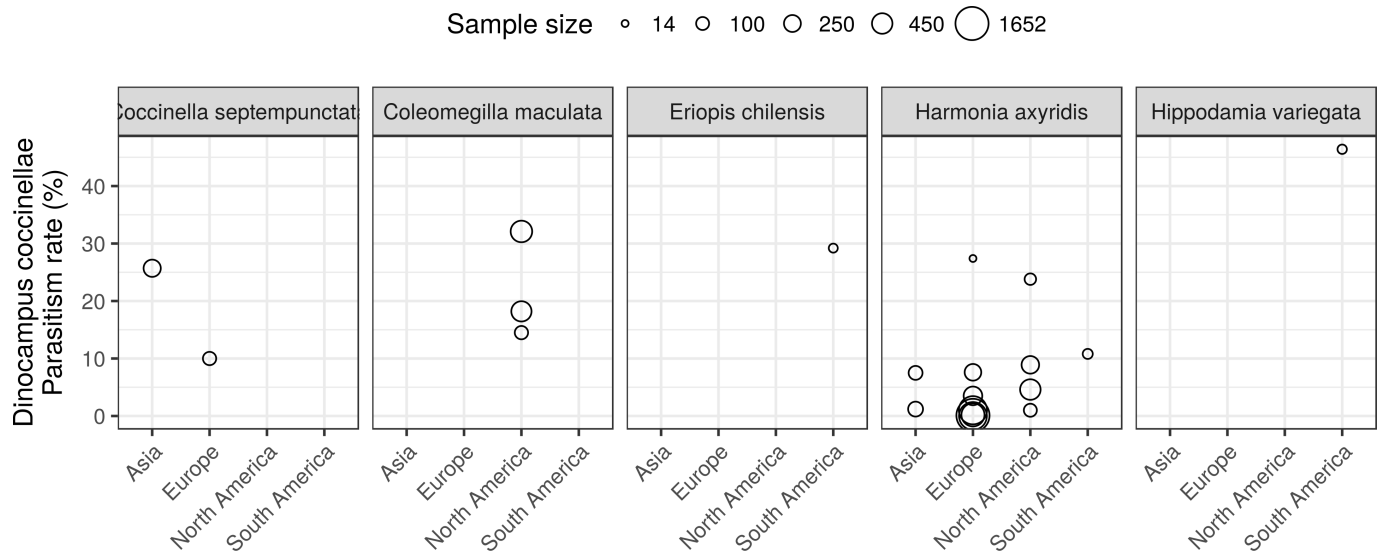The data for the other species than H. axyridis are quite scarce :

Figure 2:

We could compare the parasitism rate of H.axiridis and the parasitism rate of all other species confounded. We keep the native range data separated from the invades areas. The lines connect observations from the same study and the same year (ie data that are directly comparable).
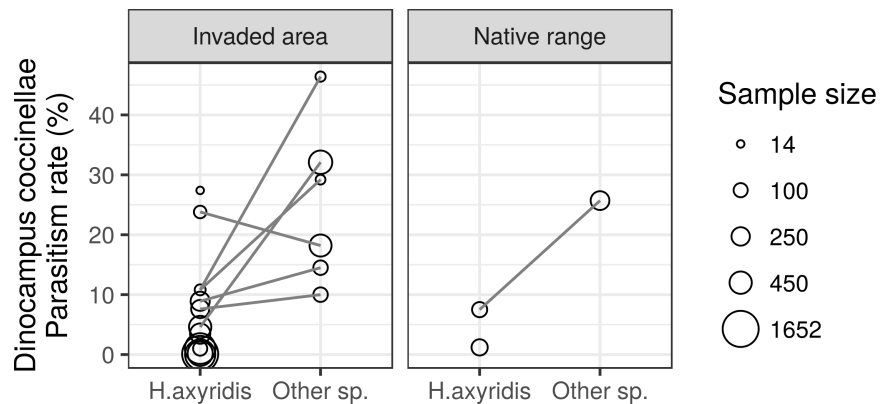

Figure 3:

2.2.2 Binomial GLMM

Is the parasitsim level different between H.axiridis and the other species ?

We used only the data from the invaded regions because the data from the native range was too scarce. We used a binomial Generalized Linear Mixed Model (GLMM) with the parasitism rate as response and the Species (H. axyridis vs Other species) as fixed explanatory variable. The study (data from one publication and one year) was used as random effect. An observation level ID was added as random effect to take into account any overdispersion.

The results show that there the other species have a significantly higher parasitism rate (binomial GLMM coefficient = 1.11, se = 0.455, z = 2.44, p = 0.0147)

Note : The overdispersion is limited in this model (~4) and excluding the observation level random effect makes the results even more significant.

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## Parasitism_rate/100 ~ Species + (1 | Study_ID) + (1 | Observation_ID)
##    Data: tmp[tmp$Range == "Invaded area", ]
## Weights: Parasitism_N
##
##      AIC      BIC   logLik deviance df.resid
##    149.4    153.0    -70.7    141.4       14
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -0.8947 -0.2081 -0.1058  0.1525  0.5394
##
## Random effects:
##  Groups         Name        Variance Std.Dev.
##  Observation_ID (Intercept) 0.4195   0.6477
##  Study_ID       (Intercept) 3.7927   1.9475
## Number of obs: 18, groups:  Observation_ID, 18; Study_ID, 12
##
## Fixed effects:
##                 Estimate Std. Error z value Pr(>|z|)
## (Intercept)      -3.8085     0.6164  -6.179 6.45e-10 ***
## SpeciesOther sp.  1.1099     0.4550   2.439   0.0147 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##            (Intr)
## SpcsOthrsp. -0.147
```

2.2.3 Paired t test by permutation

We tried a simpler approach with a paired t test using only the data for which there was both measures of parasitism for H.axiridis and other species (and repeating the data for H.axyridis when there are several other species in the same study - this is not optimal). As the parasitism rate could not be expected to follow a normal distribution we estimated the p value with a permutation test (10000 permutations), however the p value from the permutation test is quite similar to the p value of the standard paired t test.

The paired difference of parasitism level between H. axyridis and the other species in the invaded areas is close to the significance 0.05 alpha level : t = 2.16, df = 5, p = 0.0811

	t	df	p.value	perm.p.value
t	2.16	5	0.0832	0.0811

If we add the single additionnal paired data from the native range, the paired differences becomes significant :

	t	df	p.value	perm.p.value
t	2.65	6	0.038	0.0352

2.2.4 Conclusion

The data seem to consistently points toward a significantly lower level of parasitism of H. axyridis by D. coccinellae.
This is based on a variety of data collected from the literature from studies using different protocols, with different objectives and with no systematic assessment of the native fauna. So these results should be confirmed by more standardised approaches.

2.3 Changes in parasitism rate across time

The idea here was to test if there could be a time lag between the invasion and the adoption of a new host by local parasitoïds (as observed in the parasitic fungus *Hesperomyces virescens* sensu Haelewaters et al. 2017).

For the data collected during a range of years (e.g. 2004-2008), we use the mean on the range as "year".

The data don't seem to show any trend of the parasitism rate across time. However the temporal data are quite limited and probably not directly comparable. In Europe most of the data are close to the invasion start and we have less recent data.
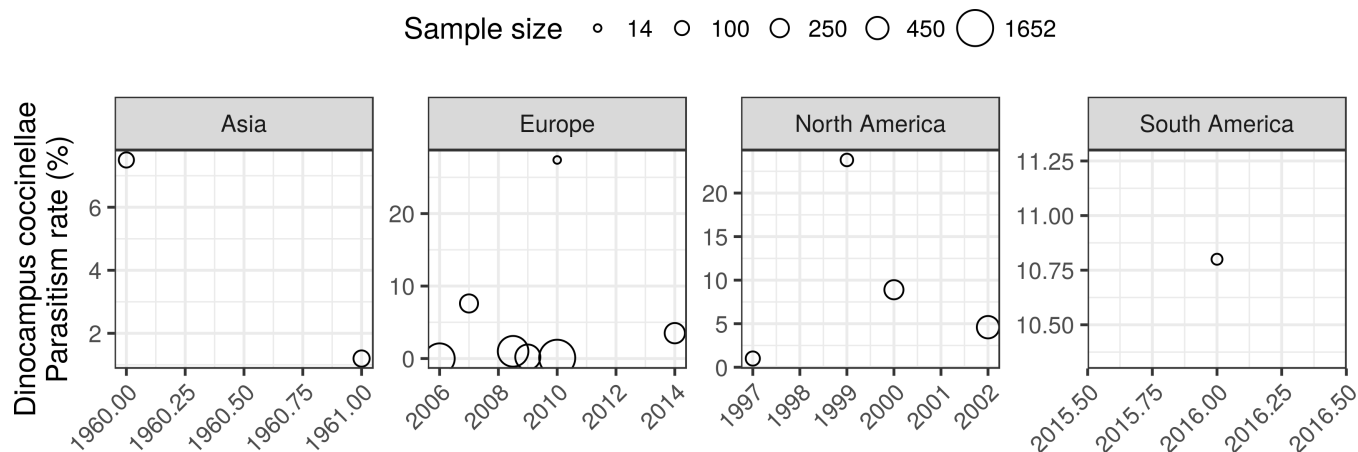

Figure 4:

3 *Dinocampus coccinellae* emergence rate

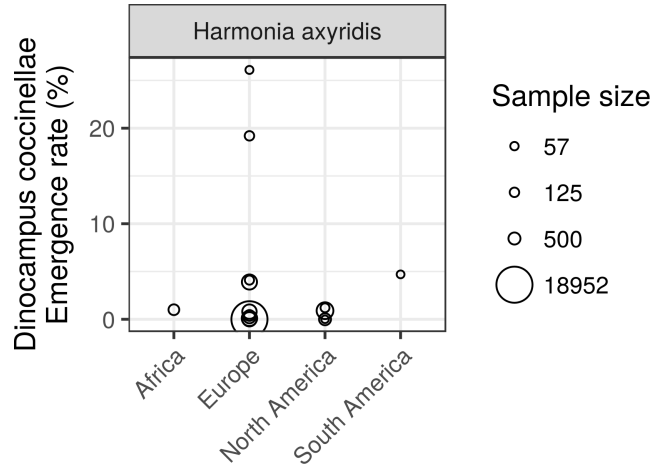## 3.1 Comparing emergence rates between regions

3.1.1 Graph

Figure 5:

3.1.2 GLM

Is the parasitism rate of H. axyridis different between regions (continents) ?

We performed a Binomial GLM with a quasilikelihood approach to estimate the overdispersion coefficient (that is quite high here : ~ 31).
There is no statistically significant difference between the regions (quasibinomial GLM, $F_{3,12} = 0.0199$, p = 0.99)
NB : we use a specific F test adapted to overdispersed GLMs instead of the more classical Likelihood Ratio Test

Table 4: Analysis of Deviance Table (Type II tests)

	SS	Df	F	Pr(>F)
Continent	11.46	3	0.01998	0.996
Residuals	2296	12	NA	NA

```
##
## Call:
## glm(formula = Emergence_rate/100 ~ Continent, family = quasibinomial,
##     data = tmp, weights = Emergence_N)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -12.640   -1.188    0.000    2.145   11.917
##
## Coefficients:
##                         Estimate Std. Error t value Pr(>|t|)
## (Intercept)             -4.5951     8.3678   -0.549    0.593
## ContinentEurope         -0.8718     8.4763   -0.103    0.920
## ContinentNorth America  -0.3217     8.9532   -0.036    0.972
## ContinentSouth America   1.5857    13.0137    0.122    0.905
##
## (Dispersion parameter for quasibinomial family taken to be 191.3224)
##
##     Null deviance: 571.27  on 15  degrees of freedom
## Residual deviance: 559.80  on 12  degrees of freedom
##   (1 observation deleted due to missingness)
## AIC: NA
##
## Number of Fisher Scoring iterations: 7
```

3.2 Comparing emergence rate between species

3.2.1 Graphs

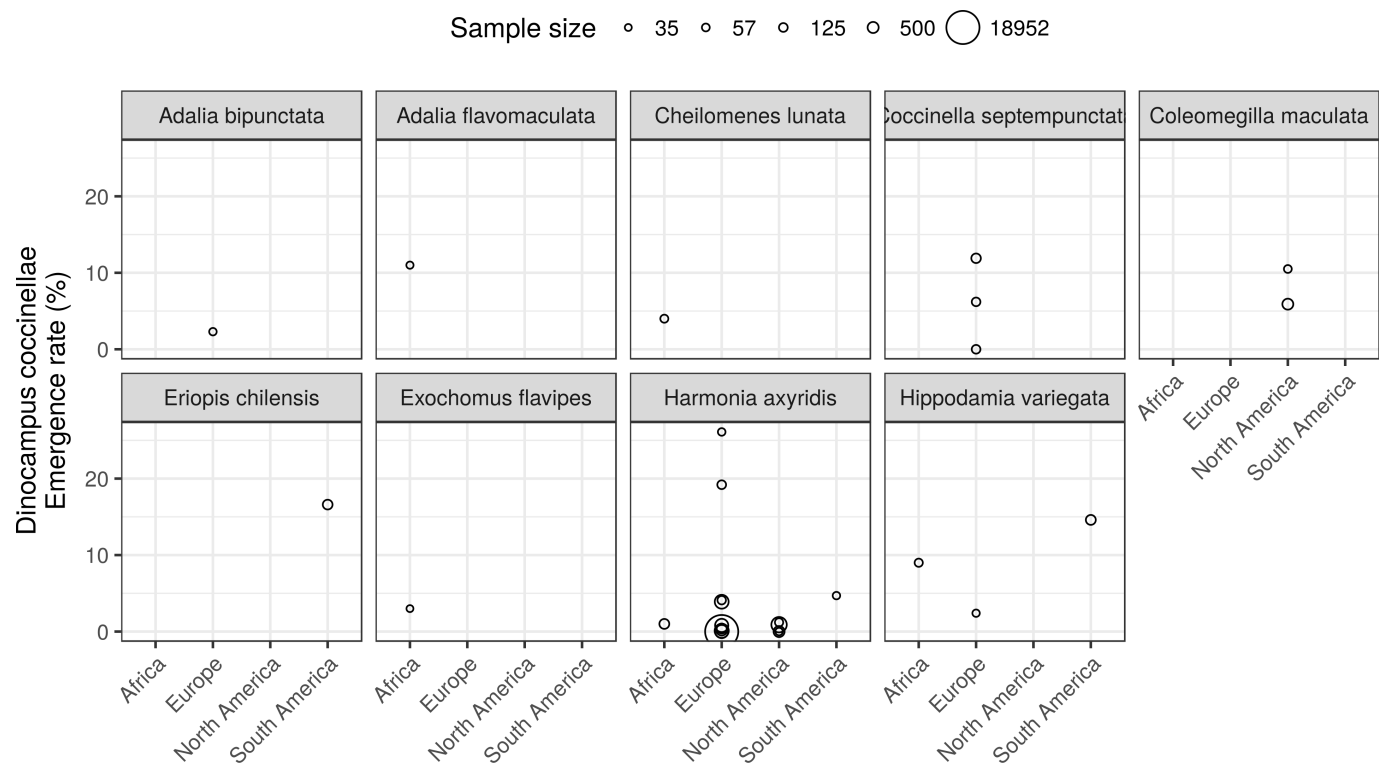The data for the other species than H. axyridis are quite scarce :

Figure 6:

We could compare the emergence rate of *H.axyridis* and the parasitism rate of all other species confounded. There are no data for emergence rate in the native area so we use only data from invaded areas. The lines connect observations from the same study and the same year (ie data that are directly comparable).
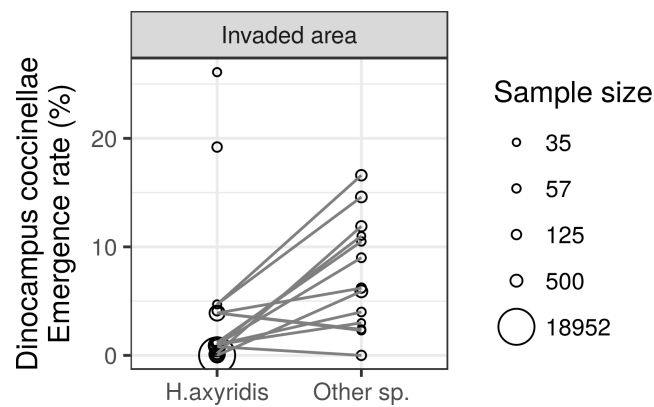

Figure 7:

3.2.2   Binomial GLMM

*Is the emergence rate different between **H.axyridis** and the other species ?*

We used only the data from the invaded regions because the data from the native range was not available. We used a binomial Generalized Linear Mixed Model (GLMM) with the emergence rate as response and the Species (*H. axyridis* vs Other species) as fixed explanatory variable. The study (data from one publication and one year) was used as random effect. An observation level ID was added as random effect to take into account any overdispersion.

The results show that there the other species have a significantly higher emergence rate (binomial GLMM coefficient = 1.85, se = 0.555, z = 3.334, p = 0.0009)

Note : The model do not converge without observation level random effects.

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##    Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula:
## Emergence_rate/100 ~ Species + (1 | Study_ID) + (1 | Observation_ID)
##    Data: tmp[tmp$Range == "Invaded area", ]
## Weights: Emergence_N
##
##      AIC      BIC   logLik deviance df.resid
##    197.8    203.2    -94.9    189.8       25
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -0.98238 -0.35960 -0.01096  0.16036  0.28588
##
## Random effects:
##  Groups         Name        Variance Std.Dev.
##  Observation_ID (Intercept) 0.9895   0.9947
##  Study_ID       (Intercept) 4.2208   2.0545
## Number of obs: 29, groups:  Observation_ID, 29; Study_ID, 16
##
## Fixed effects:
##                 Estimate Std. Error z value Pr(>|z|)
## (Intercept)      -5.1115     0.6257  -8.169 3.12e-16 ***
## SpeciesOther sp.  1.8531     0.5558   3.334 0.000856 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##            (Intr)
## SpcsOthrsp. -0.289
```

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3.2.3 Paired t test by permutation

We tried a simpler approach with a paired t test using only the data for which there was both measures of parasitism for *H.axyridis* and other species (and repeating the data for H.axyridis when there are several other species in the same study - this is not optimal). As the parasitism rate could not be expected to follow a normal distribution we estimated the p value with a permutation test (10000 permutations). The p value from the standard paired t test is provided along with the permutation test p value

The paired difference of parasitism level between *H. axyridis* and the other species in the invaded areas is significant : t = 3.8404, df = 12, p = 0.0017

	t	df	p.value	perm.p.value
t	3.84	12	0.0024	0.0017

3.2.4 Conclusion

The data seem to consistently point toward a signifianctly lower level of emergence of *Dinocampus coccinellae* when using *H.axyridis* as host relative to other species in the invaded regions. This is based on a variety of data collected from the literature from studies using different protocols, with different objectives and with no systematic assessment of the native fauna. So these results should be confirmed by more standardised approaches.

3.3 Changes in emergence rate across time

The idea here was to test if there could be a time lag between the invasion and the adoption of a new host by local parasitoïds (as observed in the parasitic fungus *Hesperomyces virescens* sensu Haelewaters et al. 2017).

For the data collected during a range of years (e.g. 2004-2008), we use the mean of the range as "year".

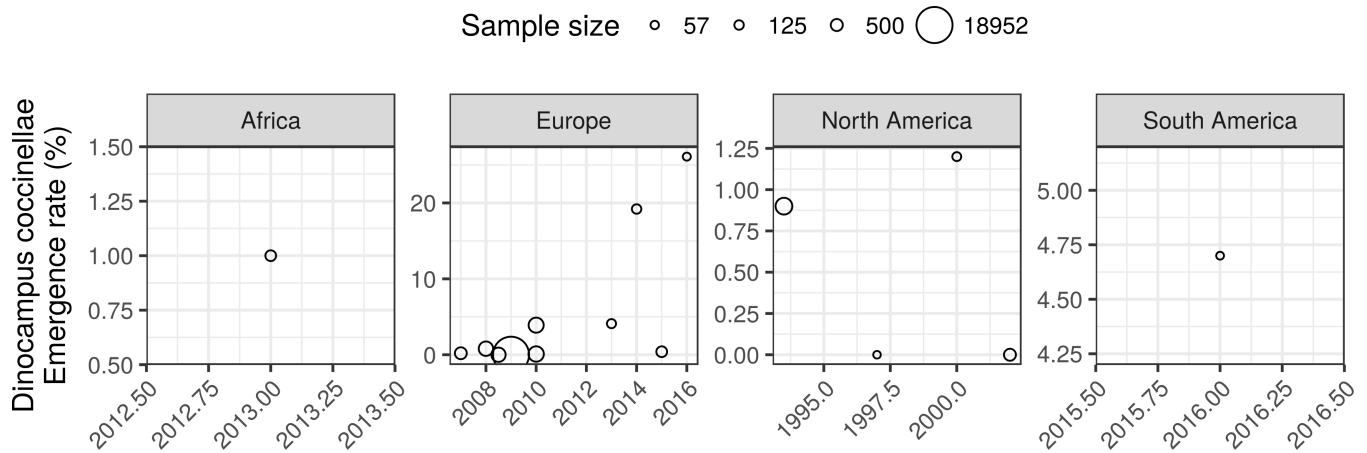The data are quite limited and don't seem to show any clear pattern

Figure 8:

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4 *Phalacrotophora spp.*

Summary of the data :

For 15 data from the native range, we have the parasitism rate but not the sample size. For the other data the minimum sample size is N = 98 and the median is N = 450. So we imputed the missing sample size with a value N = 50 which seems to be a conservative estimate. This data is only used in the binomial GLM and GLMM as weight for each observation.

```
##                    Localisation     Country    Continent            Range
##  Altai region, Russia:11     Russia :14    Asia  :16   Invaded area:18
##  London and Cambridge: 9     UK     : 9    Europe:18   Native range:16
##  Copenhagen          : 3     Denmark: 3
##  Russian Far East    : 3     England: 2
##  Bologna area        : 2     Italy  : 2
##  England             : 2     Japan  : 2
##  (Other)             : 4     (Other): 2
##     Year_start         Year                               Host
##  Min.   :1987   Min.   :1961   Harmonia axyridis        :17
##  1st Qu.:2008   1st Qu.:1968   Coccinella septempunctata: 7
##  Median :2008   Median :2004   Adalia bipunctata        : 3
##  Mean   :2005   Mean   :1991   Anatis ocellata          : 2
##  3rd Qu.:2008   3rd Qu.:2009   Harmonia quadripunctata  : 2
##  Max.   :2012   Max.   :2015   Chilocorus inornatus     : 1
##  NA's   :29                    (Other)                  : 2
##  Parasitism_rate   Parasitism_N                        Reference
##  Min.   : 0.000   Min.   :  50.0   Filatova 1974            :11
##  1st Qu.: 1.825   1st Qu.:  50.0   Ware et al. 2010         : 9
##  Median : 8.450   Median : 122.0   Kuznetsov 1987           : 3
##  Mean   :12.558   Mean   : 555.4   Steenberg & Harding 2010: 3
##  3rd Qu.:17.675   3rd Qu.: 487.5   Comont et al. 2014       : 2
##  Max.   :55.400   Max.   :4508.0   Francati 2015            : 2
##                                    (Other)                  : 4
##                     Parasitoid Imputed_N
##  Phalacrotophora fasciata:16   Mode :logical
##  Phalacrotophora spp.    :18   FALSE:19
##                                TRUE :15
##
##
##
##
```

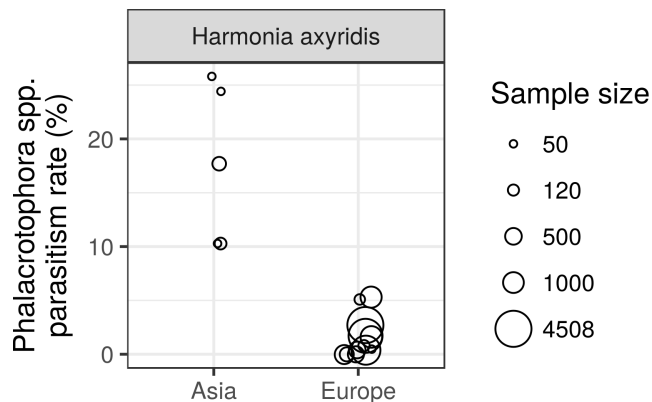## 4.1 Comparing parasitism rates between regions

4.1.1 Graph

Figure 9:

4.1.2 GLM

Is the parasitism rate of H. axyridis by Phalacrotophora spp. different between regions (continents) ?

We performed a Binomial GLM with a quasilikelihood approach to estimate the overdispersion coefficient (that is quite high here : ~ 11.5).
There is a highly significant lower parastism rate in Eyrope relative to the native range (quasibinomial GLM, $F_{1,15} = 19.68$, p = 0.0005).
NB : we use a specific F test adapted to overdispersed GLMs instead of the more classical Likelihood Ratio Test

Table 6: Analysis of Deviance Table (Type II tests)

	SS	Df	F	Pr(>F)
Continent	226.1	1	19.68	0.0004809
Residuals	172.4	15	NA	NA

```
## 
## Call:
## glm(formula = Parasitism_rate/100 ~ Continent, family = quasibinomial,
##     data = tmp, weights = Parasitism_N)
## 
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -6.5084  -2.8685  -0.8495   1.4463   6.8881
## 
## Coefficients:
##                 Estimate Std. Error t value Pr(>|t|)
## (Intercept)      -1.6290     0.3922  -4.154 0.000849 ***
## ContinentEurope  -2.3599     0.4423  -5.335 8.33e-05 ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
## 
## (Dispersion parameter for quasibinomial family taken to be 11.49099)
## 
##     Null deviance: 413.41  on 16  degrees of freedom
## Residual deviance: 187.28  on 15  degrees of freedom
## AIC: NA
## 
## Number of Fisher Scoring iterations: 5
```

4.2 Comparing parasitism rate between species

4.2.1 Graphs

The data for the other species than *H.axyridis* are quite scarce :

Figure 10:
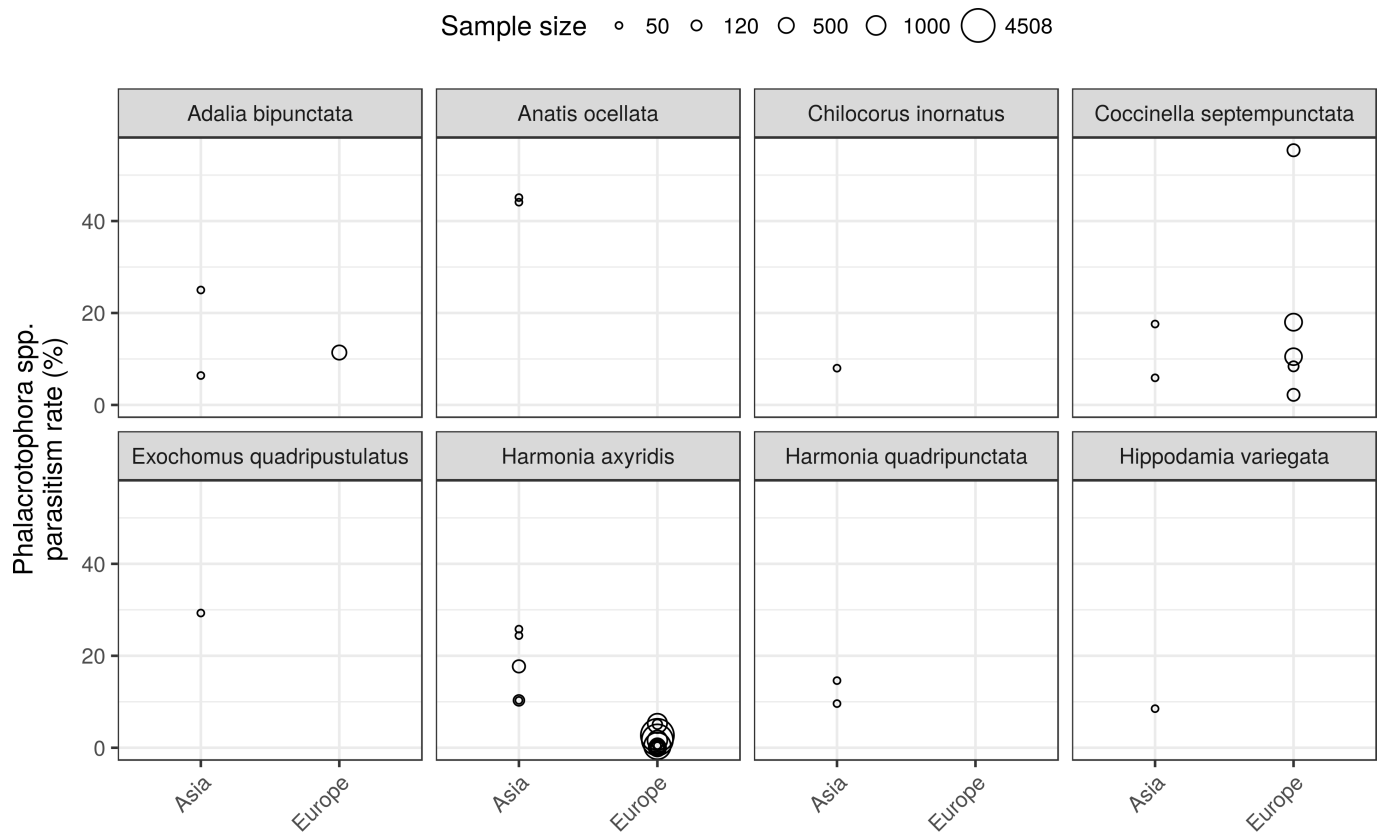
We could compare the parasitism rate of *H.axyridis* and the parasitism rate of all other species confounded. We keep the native range data separated from the invades areas. The lines connect observations from the same study and the same year (ie data that are directly comparable).

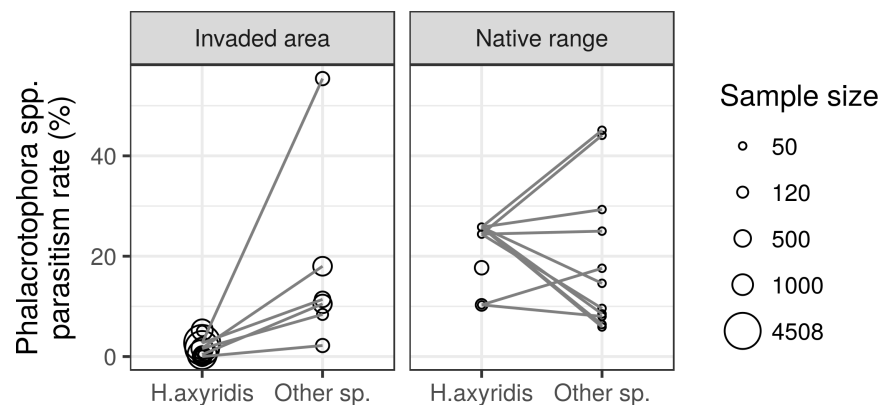NB : In the Native range, the 2 "other species" with higher parasitism rate are *Anatis ocellata*

Figure 11:

4.2.2 Binomial GLMM

Is the parasitsim level different between H.axyridis and the other species ?

In contrast with the *Dinocampus* data, we used here both the data from the invaded regions and the native range (however with an arbitrary sample size = 50 for most native range data).
We used a binomial Generalized Linear Mixed Model (GLMM) with the parasitism rate as response and the Species (*H. axyridis* vs Other species), the region (native range or invaded area) and their interaction as fixed explanatory variables. The study (data from one publication and one year) was used as random effect. An observation level ID was added as random effect to take into account any overdispersion.

The Species x region interaction is highly significant as are the Species and region main effects. In the invaded areas, the parasitism rate of *H. axyridis* tends to be lower than the other species while in the native range, the average parasitism rate is similar between H.axyridis and the other species.

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##   Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula: Parasitism_rate/100 ~ Species * Range + (1 | Study_ID) + (1 |
##     Observation_ID)
##    Data: tmp
## Weights: Parasitism_N
##
##      AIC      BIC   logLik deviance df.resid
##    258.3    267.5   -123.2    246.3       28
##
## Scaled residuals:
##      Min       1Q   Median       3Q      Max
## -1.12696 -0.25968 -0.02508  0.15102  0.71439
##
## Random effects:
##  Groups         Name         Variance Std.Dev.
##  Observation_ID (Intercept) 0.7111   0.8433
##  Study_ID       (Intercept) 0.4953   0.7038
## Number of obs: 34, groups:  Observation_ID, 34; Study_ID, 17
##
## Fixed effects:
##                                 Estimate Std. Error z value Pr(>|z|)
## (Intercept)                      -4.8673     0.3881 -12.542  < 2e-16
## SpeciesOther sp.                  2.7521     0.5058   5.441 5.29e-08
## RangeNative range                 3.2239     0.6425   5.018 5.23e-07
## SpeciesOther sp.:RangeNative range -2.8286    0.7440  -3.802 0.000143
##
## (Intercept)                     ***
## SpeciesOther sp.                ***
## RangeNative range               ***
## SpeciesOther sp.:RangeNative range ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##             (Intr) SpcOs. RngNtr
```

```
## SpcsOthrsp. -0.445
## RangeNtvrng -0.603  0.268
## SpcsOs.:RNr  0.321 -0.675 -0.540
```

% of parasitism estimated by the model for each region and group of species :

	Pct.Parasitism
SpeciesH.axyridis:RangeInvaded area	0.76
SpeciesOther sp.:RangeInvaded area	10.76
SpeciesH.axyridis:RangeNative range	16.2
SpeciesOther sp.:RangeNative range	15.19

If we use the same approach but keeping only "Coccinella septempunctata" as "other species", The results are similar excepted that the parasitism level of H.axyridis tends to be higher than the parasitism level of C. septempunctata in the native range of H.axyridis (the differences tend to be null when you mix all other species).

We can do this with C. septempunctata only because this is the only "other species" for which the quantity of data is sufficient.

```
## Generalized linear mixed model fit by maximum likelihood (Laplace
##    Approximation) [glmerMod]
##  Family: binomial  ( logit )
## Formula: Parasitism_rate/100 ~ Species * Range + (1 | Study_ID) + (1 |
##      Observation_ID)
##    Data:
## tmp[tmp$Host %in% c("Harmonia axyridis", "Coccinella septempunctata"),
##      ]
## Weights: Parasitism_N
##
##      AIC      BIC   logLik deviance df.resid
##    186.6    193.7    -87.3    174.6       18
##
## Scaled residuals:
##     Min      1Q  Median      3Q     Max
## -1.0663 -0.3716 -0.0424  0.1331  0.6458
##
## Random effects:
##  Groups         Name         Variance Std.Dev.
##  Observation_ID (Intercept) 0.3168   0.5629
##  Study_ID       (Intercept) 1.0738   1.0362
## Number of obs: 24, groups:  Observation_ID, 24; Study_ID, 17
##
## Fixed effects:
##                                    Estimate Std. Error z value Pr(>|z|)
## (Intercept)                        -4.9286     0.4086 -12.064  < 2e-16
## SpeciesOther sp.                    2.9248     0.3908   7.483 7.25e-14
## RangeNative range                   3.3008     0.6824   4.837 1.32e-06
## SpeciesOther sp.:RangeNative range -3.4128     0.7811  -4.369 1.25e-05
##
## (Intercept)                        ***
## SpeciesOther sp.                   ***
## RangeNative range                  ***
## SpeciesOther sp.:RangeNative range ***
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Correlation of Fixed Effects:
##            (Intr) SpcOs. RngNtr
## SpcsOthrsp. -0.314
## RangeNtvrng -0.599  0.188
## SpcsOs.:RNr  0.158 -0.501 -0.265
```

	Pct.Parasitism
SpeciesH.axyridis:RangeInvaded area	0.72
SpeciesOther sp.:RangeInvaded area	11.88
SpeciesH.axyridis:RangeNative range	16.41
SpeciesOther sp.:RangeNative range	10.76

4.2.3 Paired t test by permutation

We tried a simpler approach with a paired t test using only the data for which there was both measures of parasitism for H.axyridis and other species (and repeating the data for H.axyridis when there are several other species in the same study - this is not optimal). As the parasitism rate could not be expected to follow a normal distribution we estimated the p value with a permutation test (10000 permutations). We provide both the standard p value (p.value) and the permutation test p value (perm.p.value). The data from the native range and the invaded areas are analysed separately.

The difference of parasitism rate is highly significant in the invaded region :

	t	df	p.value	perm.p.value
t	2.137	5	0.0857	0.0013

In the native region, there is no significant difference ;

	t	df	p.value	perm.p.value
t	-0.7111	10	0.4933	0.4904

4.2.4 Conclusion

The data seem to consistently point toward a signifianctly lower level of parasitism of H. axyridis by Phalacrotophora spp. in the invaded areas while there is no systematic difference in the native range.
The Binomial model uses arbirary sample size for most of the native range data, however we choose a conservative value of N=50. These sample sizes are not used by the paired student tests.
This is based on a variety of data collected from the literature from studies using different protocols, with different objectives and with no systematic assessment of the native fauna. So these results should be confirmed by more standardised approaches.

4.3   Changes in parasitism across time

The idea here was to test if there could be a time lag between the invasion and the adoption of a new host by local parasitoïds (as observed in the parasitic fungus *Hesperomyces virescens* sensu Haelewaters et al. 2017).

For the data collected during a range of years, we use the mean on the range as "year". The period range and the parasitism level are very different between Asia and Europe with no overlap : the scales are completely different).

Note that the parasitism rate is not expressed in % here for technical reasons (the GLM curve needs true rates and not %)
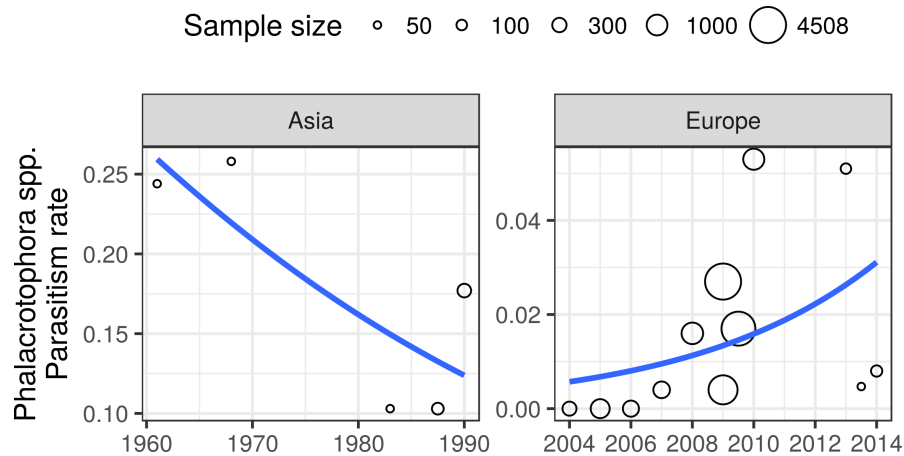

Figure 12:

We test if these trends are significant with a binomial GLM (estimated with quasilikelihood) with the Continent (Asia vs Europe), the year and their interaction as explanatory variables. Ideally we should take into account that there are repeated measures on the same country but this is not possible here because the data are too scarce.

As the aim is not to test if there is a difference of slope between the two regions we used a non standard parametrisation here. In the coefficient table, the two last lines are testing if the slope of each region is significantly different from 0 (instead of testing if they are different from each other).

In Asia, the slope is negative (-0.02311) but estimated with a high imprecision the slope is not significantly different from 0 (p = 0.4985).
In Europe, the slope is positive (0.29984) and significant but close to the 0.05 alpha level (p = 0.0381).

```
##
## Call:
## glm(formula = Parasitism_rate/100 ~ -1 + Continent + Continent:Year,
##     family = quasibinomial, data = tmp, weights = Parasitism_N)
##
## Deviance Residuals:
##     Min       1Q   Median       3Q      Max
## -6.4338  -2.2508  -1.5048   0.6666   5.3022
##
## Coefficients:
##                     Estimate Std. Error t value Pr(>|t|)
## ContinentAsia        44.21356   65.80925   0.672   0.5134
## ContinentEurope    -606.37956  260.98037  -2.323   0.0370 *
```

```
## ContinentAsia:Year       -0.02311      0.03319  -0.696    0.4985
## ContinentEurope:Year       0.29984      0.12989   2.308    0.0381 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for quasibinomial family taken to be 9.131558)
##
##     Null deviance: 18990.60  on 17  degrees of freedom
## Residual deviance:   135.94  on 13  degrees of freedom
## AIC: NA
##
## Number of Fisher Scoring iterations: 5
```

UK is the only European country with several year of data (Ware et al 2010 + Comont et al 2014). Here are the results with UK only :
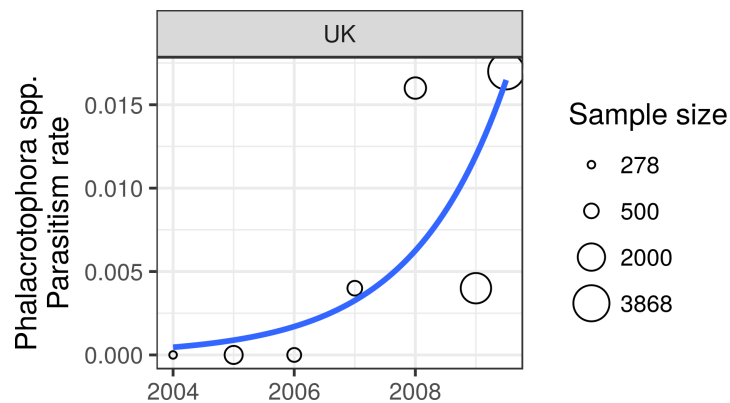

Figure 13:

This seems pretty nice but the slope is not significantly different from 0 (p = 0.161):

```
##
## Call:
## glm(formula = Parasitism_rate/100 ~ Year, family = quasibinomial,
##     data = tmp, weights = Parasitism_N)
##
## Deviance Residuals:
##      18        19        20        21        23        25        30
## -0.5905   -1.3039   -1.3362    0.1772    3.4601   -3.9400    1.1628
##
## Coefficients:
##               Estimate Std. Error t value Pr(>|t|)
## (Intercept) -1161.8236   702.8615  -1.653    0.159
## Year            0.5761     0.3498   1.647    0.161
##
## (Dispersion parameter for quasibinomial family taken to be 6.452961)
##
##     Null deviance: 63.684  on 6  degrees of freedom
## Residual deviance: 32.714  on 5  degrees of freedom
## AIC: NA
##
```

```
## Number of Fisher Scoring iterations: 5
```

Conclusion : there seem to be a weak trend toward an increased parasitism rate in Europe but this is very weak and clearly would need more longitudinal and comparable data. . .

5 References and Session information

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Session information

```
## R version 3.4.1 (2017-06-30)
## Platform: x86_64-pc-linux-gnu (64-bit)
## Running under: Ubuntu 16.04.3 LTS
##
## Matrix products: default
## BLAS: /usr/lib/libblas/libblas.so.3.6.0
## LAPACK: /usr/lib/lapack/liblapack.so.3.6.0
##
## locale:
##  [1] LC_CTYPE=en_GB.UTF-8       LC_NUMERIC=C
##  [3] LC_TIME=en_GB.UTF-8        LC_COLLATE=en_GB.UTF-8
##  [5] LC_MONETARY=en_GB.UTF-8    LC_MESSAGES=fr_BE.UTF-8
##  [7] LC_PAPER=fr_BE.UTF-8       LC_NAME=C
##  [9] LC_ADDRESS=C               LC_TELEPHONE=C
## [11] LC_MEASUREMENT=fr_BE.UTF-8 LC_IDENTIFICATION=C
##
## attached base packages:
## [1] stats     graphics  grDevices utils     datasets  methods   base
##
## other attached packages:
## [1] lme4_1.1-13       Matrix_1.2-11     reshape_0.8.6
## [4] car_2.1-5         ggplot2_2.2.1.9000 pander_0.6.0
## [7] knitr_1.16
##
## loaded via a namespace (and not attached):
##  [1] Rcpp_0.12.12       compiler_3.4.1     nloptr_1.0.4
##  [4] plyr_1.8.4         tools_3.4.1        digest_0.6.12
##  [7] evaluate_0.10.1    tibble_1.3.4       gtable_0.2.0
## [10] nlme_3.1-131       lattice_0.20-35    mgcv_1.8-19
## [13] rlang_0.1.2        yaml_2.1.14        parallel_3.4.1
## [16] SparseM_1.77       withr_2.0.0        stringr_1.2.0
## [19] MatrixModels_0.4-1 rprojroot_1.2      grid_3.4.1
## [22] nnet_7.3-12        rmarkdown_1.6      bookdown_0.4
## [25] minqa_1.2.4        magrittr_1.5       codetools_0.2-15
## [28] backports_1.1.0    scales_0.5.0.9000  htmltools_0.3.6
## [31] MASS_7.3-47        splines_3.4.1      pbkrtest_0.4-7
## [34] colorspace_1.3-2   labeling_0.3       quantreg_5.33
## [37] stringi_1.1.5      lazyeval_0.2.0     munsell_0.4.3
```