EPIGENETICS AND HOST ADAPTATION

ANNEMARIE JELLEMA
S1617141
RIJKS UNIVERSITEIT GRONINGEN
11-10-09

Abstract. *Invasive species can have an enormous effect on their surroundings in various ways. They have effects on human health and other species. Local adaptation by native species can occur,* Rhagoletis pomonella *and* Jadera haematoloma*. Recent studies show this can be achieved by other pathways than only DNA variation. Epigenetics, heritable changes in gene expression not explained by the DNA, plays a part to. DNA Methylation, probably the best studied epigenetic mechanism, causes gene silencing. Chromatin remodeling is proposed as a form of epigenetics. Histone acetylation is a more recent studied system and the final pathway is RNA mediated gene silencing. Most of the before mentioned pathways are poorly studied in relatedness to insect and host adaptation. Studies show that the effects of methylation in insects have different outcome. Computer models on the effect of plastic response and adaption show different effects with different circumstances. However when relating the above with adaptation to invasive species, it appears that epigenetics can play a positive role.*

INTRODUCTION

Invasive species can have an enormous effect on their surroundings in various ways. Invasive species can have a negative effect on the human health and can enhance a safety risk. But they also have great effects on the native ecosystem by negatively influencing soil nutrience, light regimes or water supplies they can supress native species. Thus they create a new composition of species.
A currently important example is the *Ambrosia artemisiifolia*. This plant has a late blossoming period in September and October. The pollen it produces are known to cause hay fever. Because of the late blossoming period the hay fever period can be extended by 2 months. This brings a health risk along with a lot of medical costs (Taramarcaz et al 2005).
Another example is the plant *Lantana camara* which is invasive in Australia. Where it reduced the densities of juvenile common sub canopy species. This has great consequences for species richness, abundance and composition. It has been shown that sites invaded with *L. camara* have led to a reduction in specie richness and changes the species composition. What is causing these declines is not clear yet (Gooden et al 2009).
Also local adaptation by native species can occur. The larvae of the apple maggot fly (*R. pomonella*) naturally occurred on the native hawthorn (Crataegus spp) but shifted to the non-indigenous apple. There are now two genetically distinct populations that are partially reproductively isolated (Feder et al 1988). Another example of this is the soapberry bug (*J. haematoloma*) native to north America. The soapberry bug originally foraged on the balloon vine (*Cardiospermum corindum*) and the soapberry tree (*Sapindus saponaria v. drummondii*). There the bug uses his long needle like beak to penetrate through the fruit into the core where it feeds upon the seeds. Three new species were introduced into the natural habitat of the soapberry bug, namely the round-podded and flat-podded golden rain tree (*Koelreuteria paniculata* and *Koelreuteria elegans*) and the heartseed vine (*Cardiospermum halicacabum*). The soapberry bug shifted from their native hosts onto these new possible hosts plants. All these plants vary in the thickness of their fruit walls (Carroll and Boyd 1992). The soapberry bug has adapted to the new hosts by adapting their beak length to the thickness of the fruit walls. So the introduction of these new species caused genetic variation and might end in speciation (Carrol et al 2001). This shows an

impact on the native ecology by non-native species.
Because of various emotional values people and readers give to the existing terms in invasion ecology, I would like to present my definitions. The definitions I use are proposed by Falk-Petersen et al (2005) the most important are summed up in table 1.
So local adaptation by native species to new non-native species exists, see above at the *R. pomonella* and *J. haematoloma* . But what drives these adaptations. What makes is possible for species to shift to new hosts. What is the underlying pathway? Of course is genetic variation a logical statement. Variation in the DNA can cause phenotypic differences where evolution can act on. This has been studied in various insects, *R. pomonella* (Feder Filchak 1999), *Oreina Elongata* (Ballabeni et al 2003), *Tephritis conura* (Diegisser 2007), *J. haematoloma* (Carrol et al 2001) and many more. They gave closely related conclusions but sometimes with small differences. The primairy conclusion is that host adaptation is driven by genetic differentiation, however some studies are inconclusive leaving a small unexplained part (Ballabeni et al 2003, kawecki 1995).

Term	Proposed definition
Native/ indigenous/ original	An organism occurring within its natural past or present range and dispersal potential (organisms whose dispersal is independent of human intervention)
Non-native/ alien/ adventive/ exotic/ foreign/ introduced/ non-indigenous/ novel	An organism occurring outside its natural past or present range and dispersal potential including any parts of the organism that might survive and subsequently reproduce (organisms whose dispersal is caused by human action)
Introduction	Direct or indirect movement by human agency, of an organism from its native past or present range to a range outside its distribution potential
Escape	Non-native organism, or part of organism that might survive and subsequently reproduce, originally domesticated, now found in the wild
Established	Native or non-native organism that has obtained a self-sustaining population in an area it previously did not occur
Naturalized	A non-native organism that has obtained a self-sustaining population
Invasive	Alien organisms that have established in a new area and are expanding their range
Pest	Organisms considered harmful to human activities
Transformers	Organisms that change the character, condition, form or nature of a natural ecosystem over a substantial area

Table 1. Modified from Falk-Petersen et al (2005).

EPIGENETICS

Recent studies show there are more pathways then just by DNA variation. There has been a more recently development in evolution theories, epigenenetics. Epigenetics is the study of heritable changes in gene expression and function that cannot be explained by changes in the underlying DNA sequence (Richards 2006, Bird 2007). Could this play a role in faster adaptation, or is it a constrain to actual speciation. To what extend has epigenetics a positive or negative role on new host adaptation.
What exactly is epigenetics, it's the heritable changes in gene expression not explained by the DNA that's already been said, but what are the pathways now known on how it works. Pàl and Hurst explain in chapter 16 in the book "Organelles, Genomes and Eukaryote Phylogeny: An Evolutionary Synthesis in the Age of Genomics" four pathways.

- DNA Methylation
- Chromatin remodeling
- Histone Acetylation
- RNA-mediated Gene Silencing

DNA Methylation, probably the best studied epigenetic mechanism, causes gene silencing by methylating cytosine to 5-methylcytosine. The percentage in methylated cytosines in insects is not very high, certainly not when compared to vertebrates and plants (Adams 1996). But this is also research dependant because processes in invertebrates seem to be different from vertebrates. Stages in which there are methylated cytosines can differ. Lyko et al (2000) mainly found 5-methylcytosine in the early embryonic development in *Drosophila melanogaster*. However the methylation process does not seem to be restricted to the CpG dinucleotides but also occurs in CpA and Cpt.
Chromatin remodeling is proposed as a form of epigenetics. It also causes a form of gene silencing. The way this is being achieved is closely related to the methylation process. Certain chromatin proteins have the ability to bind to DNA regions and each other. This can cause a new folding structure that can be inherited. There is little information on chromatin remodeling in insects or host adaptation. There are some studies done on Drosophila sp. that clearly show that chromatin remodeling does exist (Lyko and Paro 1999).
Histone acetylation is a more recent, poorly, studied pathway for epigenetics (Turner 2000). It reduces the affinity of the H4 histone protein to DNA, leading to relaxed chromatin structure and higher transcription rates. So where methylation causes gene silencing, acetylation causes a higher transcription rate of the DNA. In reverse where demethylated DNA has a higher transcription rate, deacetylated DNA causes condensed DNA with now or limited transcription. This pathway has been studied in insects though not much (Wolf 1996) and nothing at all related to host adaptation. The main founding is that acetylation is mostly responsible for leveling gene expression between 2 chromosomes, to prevent over active transcription.
RNA mediated gene silencing happens when small RNA's, derived from cleavage of double stranded RNA, become involved in posttranscriptional gene silencing. This has been studied

in plants (Matzke 2001). However there is little information and all these pathways are interconnected to each other.

EPIGENETICS AND HOST ADAPTATION.

So most of the before mentioned pathways are poorly studied in relatedness to insect and host adaptation. The best studied system is DNA methylation, so other pathways might be used by insect species, there just not studied yet or very poorly.
Field et al (2004) shows the amount of studies done on DNA methylation in insect orders, see table 2. This shows that most research has been done on the Diptera and the Homoptera, even though this is a very small amount. Other orders get even less attention. So the data is too incomplete to make any suggestions as to whether the methylation processes might be conserved in orders or families. More research should be done on epigenetic processes in different families to see if there is any irrelativeness between the success of families and epigenetic pathways.

Order	Species
Coleoptera (beetles)	Not determined
Diptera (flies)	Aedes albopticus
	Culex tritaeniorhynchus
	Drosophila melanogaster
	Drosophila pseudoobscura M
	Anopheles gambiae
Hemiptera (bugs)	Not determined
Homoptera (aphids, cicadas, scales)	Planococcus citri
	Planococcus obscurus
	Planococcus calceolariae
	yzus persicae
	Megoura viciae
	Schizaphis graminum
Hymenoptera (bees, ants, wasps)	Not determined
Lepidoptera (butterflies, moths)	Bombyx mori
	Mamestra brassicae
Odonata (dragonflies and damselflies)	Not determined
Orthoptera (grasshoppers, crickets)	Grylloptalpa fossor
	Acheta domesticus

Table 2 from Field et al 2004

However there are some studies showing that the effects of methylation in insects have different outcome (Field et al 2004). The stage at which the process occurs differs amongst different insect species. As an example, a long time it was thought there was no, or very little, methylation in drosophila sp. All studies focused on the adult fase of the fly. However Lyko et al (2000) showed that there was methylation in *D. melanogaster*. The methylation occurred early in the larval stage. He found a 0.4% methylation in young embryos (1-2 h) and 0.1% in older embryos (15-16 h), this suggests that it plays a part in the development of a individual. Also Field (2000) showed that in *Myzus persicae* methylation plays a part in the resistance against insecticides. This shows another effect of the methylation process.
So epigenetics has different functions in different taxa's. Another function of epigenetics might be a fast adaptation to new host species. Adaptation trough epigenetics is visible in phenotypic plasticity. A very recent study shows that *Brevicoryne brassicae* is plastic to different environments (Leal-Aguilar et al 2008). This aphid can adapt to Brassica oleraceae and Brassica campestris where it feeds on. The plastic response is on the nitrogen level (nutrition value) of the different host species. This shows a sort of fine tuning on the small scale that influences adaptation on a more rough scale. This would indicate that plastic phytophagous insect species could adapt quicker to new host species than species without plastic responses.
There are computer models on the effect of plastic response and adaption showing different outcome depending on the rules (Price et al 2003). Independent of a changing environment a plastic response could lead to a phenotype where selection could cling on to. So the initial cue is a plastic response to something. The response that arises, a changing phenotype, then could be picked up by selection. Then if selection favors this plastic trait it could lead to speciation. This is an example of genetic assimilation. Genetic assimilation means that an incomplete plastic trait can push a population into a general direction after which selection "takes over". But when the environment is stable and the two adaptation peaks lay close together, plastic responses will lead to one plastic population. So whether plastic responses are positive or negative to speciation depends on the specific circumstances.

CONCLUSION

However when relating the above with adaptation to invasive species, it appears that epigenetics can play a positive role. It could place phytophagous insect species into the right direction after which it depends on the circumstances whether it would lead to speciation. When the new host has a high resemblance to the old host the transition is quicker and being plastic would have a positive effect, but no speciation will occur. When the new host species has a lower resemblance to the old host epigenetics would be positive in pushing into the right general direction. However it will be difficult to maintain a population when the extremes get to extreme and speciation should occur.

REFERENCES

Ballabeni, P., Gottbard, K., Kayumba, A., Rahier, M., 2003. Local Adaptation and Ecological Genetics of Host-Plant Specialization in a Leaf Beetle. *Oikos*, 101 (1), pp.70-78.

Bird, A., 2007. Perceptions of Epigenetics. *Nature*, 447 (7143), pp.396-398.

Carroll, S. P., Dingle, H., Famula, T. R., Fox, C. W., 2001. Genetic Architecture of Adaptive Differentiation in Evolving Host Races of the Soapberry Bug, Jadera Haematoloma. *Genetica*, 112 pp.257-272.

CARROLL, S., BOYD, C., 1992. Host Race Radiation in the Soapberry Bug - Natural-History with the History. *Evolution*, 46 (4), pp.1052-1069.

Diegisser, T., Seitz, A., Johannesen, J., 2007. Morphological Adaptation in Host Races of Tephritis Conura. *Entomologia Experimentalis Et Applicata*, 122 (2), pp.155-164.

Falk-Petersen, J., Bohn, T., Sandlund, O. T., 2006. On the Numerous Concepts in Invasion Biology. *Biological Invasions*, 8 (6), pp.1409-1424.

Feder, J. L., Filchak, K. E., 1999. It's About Time: The Evidence for Host Plant-Mediated Selection in the Apple Maggot Fly, Rhagoletis Pomonella, and Its Implications for Fitness Trade-Offs in Phytophagous Insects. *Entomologia Experimentalis Et Applicata*, 91 (1), pp.211-225.

FEDER, J., CHILCOTE, C., BUSH, G., 1988. Genetic Differentiation Between Sympatric Host Races of the Apple Maggot Fly Rhagoletis-Pomonella. *Nature*, 336 (6194), pp.61-64.

Field, L. M., 2000. Methylation and Expression of Amplified Esterase Genes in the Aphid Myzus Persicae (Sulzer). *Biochemical Journal*, 349 (Part 3), pp.863-868.

Field, L. M., Lyko, F., Mandrioli, M., Prantera, G., 2004. DNA Methylation in Insects. *Insect Molecular Biology*, 13 (2), pp.109-115.

Gooden, B., French, K., Turner, P. J., 2009. Invasion and Management of a Woody Plant, Lantana Camara L., Alters Vegetation Diversity Within Wet Sclerophyll Forest in Southeastern Australia. *Forest Ecology And Management*, 257 (3), pp.960-967.

KAWECKI, T., 1995. Expression of Genetic and Environmental Variation for Life-History Characters on the Usual and Novel Hosts in Callosobruchus-Maculatus (coleoptera, Bruchidae). *Heredity*, 75 (Part 1), pp.70-76.

Leal-Aguilar, K., Ruiz-Montoya, L., Perales, H., Morales, H., 2008. Phenotypic Plasticity of Brevicoryne Brassicae in Responses to Nutritional Quality of Two Related Host Plants. *Ecological Entomology*, 33 (6), pp.735-741.

Lyko, F., Paro, R., 1999. Chromosomal Elements Conferring Epigenetic Inheritance. *Bioessays*, 21 (10), pp.824-832.

Lyko, F., Ramsahoye, B. H., Jaenisch, R., 2000. Development - DNA Methylation in Drosophila Melanogaster. *Nature*, 408 (6812), pp.538-540.

Matzke, M. A., Matzke, A. J. M., Pruss, G. J., Vance, V. B., 2001. RNA-Based Silencing Strategies in Plants. *Current Opinion In Genetics & Development*, 11 (2), pp.221-227.

Pál, C., Hurst, D.L., 2004. Epigenetic Inheritance and Evolutionary Adaptation. In R.P. Hurt, D.S. Horner, ed. 2004. *Organelles, Genomes and Eukaryote Phylogeny: An Evolutionary Synthesis in the Age of Genomics*. Systematics association. Ch.16

Price, T. D., Qvarnstrom, A., Irwin, D. E., 2003. The Role of Phenotypic Plasticity in Driving Genetic Evolution. *Proceedings Of The Royal Society Of London Series B-biological Sciences*, 270 (1523), pp.1433-1440.

Richards, E. J., 2006. Opinion - Inherited Epigenetic Variation - Revisiting Soft Inheritance. *Nature Reviews Genetics*, 7 (5), pp.395-U2.

Taramarcaz, P., Lambelet, C., Clot, B., Keimer, C., Hauser, C., 2005. Ragweed (Ambrosia) Progression and Its Health Risks: Will Switzerland Resist This Invasion? *Swiss Medical Weekly*, 135 (37-38), pp.538-548.

Turner, B. M., 2000. Histone Acetylation and an Epigenetic Code. *Bioessays*, 22 (9), pp.836-845.

Wolf, K. W., 1996. The Structure of Condensed Chromosomes in Mitosis and Meiosis of Insects. *International Journal Of Insect Morphology & Embryology*, 25 (1-2), pp.37-62.