# Plant – herbivore relationships



VOJTECH NOVOTNY: COMMUNITY ECOLOGY, LECTURE NO 2 University of S. Bohemia

#### Modes of exploitation:

• Grazers: one grazer negatively impacts many individuals



many herbivores (also flower nectar robbers ...)

• Predators: one predator kills many individuals



many carnivores, also seed-eating herbivores ...

• Parasites: one parasite impacts one individual



macroscopic parasites, pathogens incl. plants...

• Parasitoids: one parasitoid kills one individual



insect parasitoids Hymenoptera...

# Why is the world green?

Herbivores are controlled by

- their enemies (top-down control): "world is green"
- their plant resources (bottom-up control): "world is green but the greens taste awful"





#### Herbivory is rather old...



Furstenberg-Hagg et al. Int. J. Mol. Sci. 2013, 14, 10242

#### Insects herbivores: the most species-rich herbivore group

(although recent DNA barcoding may boost parasitoid Hymenoptera and sarcophagous Diptera numbers)



Bronwyn Officen





#### Relative consumption rate of caterpillars vs. leaf water & nitrogen



Aphid Acyrtosiphon pisum and bacterium Buchnera aphidicola from its mycetocyte

Cecidomyid fly Asteromyia carbonifera and galls with Bostryosphaeria fungus

Termites and a protozoan *Trichonympha flagellate* from their guts, decomposing cellulose



Poor quality of plants leads to various mutualisms with fungi, bacteria and protozoans, helping herbivores to digest plant matter





Ambrosia beetles and *Ophiostoma clavigerum*, one of fungi from their galleries

Janson et al. 2008, Evolution 62:997





Principal small-molecule secondary metabolites in plants







Molecular networks for invasive and native species in a temperate deciduous forest in Maryland, USA forest plot. Nodes represent compounds; links between nodes indicate molecular structural similarity between compounds.



#### AILANTHUS ALTISSIMA

LONICERA JAPONICA



# 

LONICERA MAACKII

The most abundant compounds unique to each invasive species



Sedio et al. Ecology and Evolution. 2020;10:8770–8792

## Cardenolide sequestration in Asclepias herbivores



Cardenolide

Oncopeltus fasciatus



Agrawal et al. New Phytologist (2012) 194: 28

## Ecological correlates of qualitative x quantitative mode of defense

	quantitative	qualitative
Examples	cellulose	alkaloids
	hemicellulose	toxic amino acids
	lignins	cyanogens
	tannins	glucosinolates
	silica	terpenoids
Ecological	large polymer molecules	small toxic molecules
traits	immobile	mobile
	costly to produce	cheap to produce
	effective in large doses	effective in small doses
	present in long-lived tissues	present in growing tissues
	present in apparent plants	present in unapparent plants
	effective against most herbivores	effective against generalists



Endospermum plants - Camponotus ants, New Guinea



Macaranga plants - Crematogaster ants, South East Asia



Mutualistic ants: biological defense



Thorns – mechanical defense

Latex – mechanical and/or toxic defense

#### How to circumvent latex defence: leaf trenching

Trenching of aroid leaves [Alocasia, Colocasia] by chrysomelid beetle [Aplosonyx ancora]



#### Darling, 2007. Biotropica 39: 555–558

FIGURE 1. Circular trenching of avoid leaves (Asceace) by Aplanoys amount (Chrysonelidae). (A) Heavily damage leaf of Adoxia amointarias. (B) Leaf of Colocaia gignaros with circular trenchines. (C) Lates exoding from parity areas trenched leaf of Adoxia singipanos. (D) Beetle and Almost completely common block on Colocaia gignaros. (E) Beetle and feeding damage on heavily aracked leaf of Adoxia amointarias (A), E) Car Humong National Park (C). (D) Be be National Park (B) Beetle Ad

#### Production of secondary metabolites is costly...



Leaf fibre content (%)



## Cecropia

... but it works (sometimes)

#### Operophtera brumata

Fig. 3.17 Relationship between tannin concentration in the foliage of *Cecropia* and the number of leaves produced per plant. Investment in tannin appears to occur at the expense of leaf production, and may represent the cost of defence. (From Coley 1986, with permission from Springer-Verlag New York,



Haak et al. Proc. R. Soc. B (2012) 279, 2012–2017

Three plant strategies:

• high investment in growth and low in defense in resource-rich environment

-- apparent plants: tolerance to herbivory

-- unapparent plants: escape from herbivory in time or space

• low investment in growth and high in defense in resource-poor environment



#### Finding a rare host plant: difficult in diverse vegetation



Fig. 10-7 Mean number of striped cucumber beetles (Acalymma vitata) on cucumber plants (Cucumis sativus) in garden plots in monocultures, or in polycultures planted with corn (Zea mays) and broccoli (Brassica oleracea). Density of cucumber plants (289 or 144/100 m<sup>2</sup>), by itself, has little influence on beetle density. (•—•••) Monoculture high density; (o—•••) monoculture low density; (•=--••) polyculture high density; (o=--••) polyculture high density; (o=--••) polyculture low density. After Bach (1980).



Number of plant species per 1000 km<sup>2</sup>

## Mass fruiting and seed predator saturation: *Quercus robur* and cynipid wasp *Andricus quercuscalicis* in UK



Crawley & Long Journal of Ecology 1995, 83, 683-696

Mass fruiting and seed predator saturation: *Larix* trees and *Strobilomyia* flies in the French Alps



Heavy crop = lower % predation



Strobilomyia



Poncet et al. Oecologia (2009) 159:527–537

Pioneer apparent plants: the main enemy is other plants; the herbivores are thus "ignored" (and tolerated)



(i) species adapted to resource-rich environments have intrinsically faster growth rates than species adapted to resource poor environments

(ii) fast-growing species have shorter leaf lifetimes than slow-growing species

(iii) fast-growing species have lower amounts of constitutive defences than slow-growing species

(iv) fast-growing species support higher herbivory rates than slow-growing species



## ... although herbivory is still costly.



Fig. 4-2 Effects of leaf area removal from *Piper arieianum* shrubs on seed production 1 year (left) and 2 years (right) after a single defoliation in Costa Rica. Partial defoliation has lasting effects on both seed number and viability. This experiment simulates natural weevil (*Perdileftus* sp.) Ambetes sp.) herbivory. Aiter Marquis (1984).



Epiphytic orchids & bromeliads: extremely well-defended plants in low-resource environment





Leaf economics spectrum: one-dimensional trend in correlated traits



# And now for something completely different

#### Induced defense



Induced defence can be advantageous, as investment takes place only when there is a real risk of herbivory, but sometimes can come too late



#### Epirrita autumnata



#### Betula pubescens



Fig. 4-9 Survival and fecundity of moth larvae (*Epirrita autumnata*) on leaves of birch trees (*Betula pubescens spp. tortuosa*). Either leaf damage or application of caterpillar droppings (frass) increases the resistance of the trees, and consequently decreases correlates of moth fitness. Bars indicate standard deviations. After Haukioja et al. (1985b).

## How plants cry for help: signalling herbivory to predators







#### E. MÄNTYLÄ, K. SAM , A. HUMLOVA



Mrazova & Sam 2017. Arthropod-Plant Interactions DOI 10.1007/s11829-017-9558-9
Discoveries of the effects of herbivore induced volatile organic compounds



Discovery of the herbivore induced volatile organic compound (HI-VOC) receivers:

- other plants
- predatory mites
- parasitoid wasps
- predatory bugs
- predatory lady beetles
- herbivorous moths, which are repelled
- parasitic plants
- nematodes
- systemic parts of the same plant
- predatory birds
- resistance to pathogens

## Leaf damage increases attack rate on caterpillars by birds and ants along altitudinal gradient in tropical forest





Tvardikova & Novotny 2012 J Trop Ecol.

Costs of mobile and immobile defenses: mobile defenses have to be produced constantly, immobile last for long time



Leaf lifetime (months)

Defended vs. non-defended plants: a game

	Defended	Non-defended
	p	1-p
Defended	hB-hH-C	hB- <mark>hH</mark> -C
Non-defended	hB-hH-C	hB-hH-C

h = probability of herbivory, H = fitness cost of herbivore damage, C = cost of defence, B = competitive benefit from the opponent being damaged by herbivores; orange terms are zero;
p = frequency of defended plants in the population

-pC + (1-p)(hB-C) = -phH + (1-p)(hB-hH)

-pC+hB-C-phB+pC = -phH+hB-hH-phB+phH

C = hH

http://www.ibiblio.org/herbmed

Caffeine: one of the ecologically most successful alkaloids enabling *Coffee arabica*, via a mutualistic relationship with a vertebrate species, to outcompete hundreds of plant species









# And now for something completely different

## Young vs. mature leaves: unapparent high-quality vs. apparent low-quality resources







Defense of maturing bracken fern leaves



Pteridium aquilinum, UK



Feeding on young leaves is costly for the plant

Photosynthetic production of a population of leaves that
(a) has no mortality
(b) mortality risk increases with leaf age
[usual physiological pattern]
(d) mortality risk is constant
(e) mortality decreases with leaf age
[high herbivory pattern]



Fig. 3. The effects that different patterns of leaf survivorable would have on the rate of "reprodución" of fixed carbon. I survivorable curves are shown on a logarithme scale. a The use of the transmission of the scale state of the scale s

## Young leaf: a precious resource difficult to defend



Young leaf characteristics for species with 'escape' and 'defense' syndromes

	Escape	Defense
Herbivory	high	low
Toughness	low	low
Leaf expansion rate	fast	slow
Nitrogen for growth	high	low
Chemical defenses	low	high
Chloroplast development	delayed	normal
Nitrogen for greening	low	high
Synchrony of leaf production	high	low

Kursar & Coley 2003





Delayed greening: faster expansion with lower N concentrations



Kursar & Coley 2003 Kursar et al. PNAS 2009;106:18073-18078





Tropical herbivory: young leaf is the critical stage

Kursar & Coley 2003

# And now for something completely different



## Herbivores determine plant competitive hierarchy

reciprocal transplants of plants between clay and white sands in tropical forest

clay plants do better on clay than white-sand plants

#### but

white-sand plants do better on white-sand only when insect herbivores are present

Fine et al. 2004, Science 305: 663

## Top-down control: birds and bats control arthropods on tropical foliage



(A) Mean number of arthropods per m2. (B) Mean herbivory as percent of total leaf area.(C) Micronycteris microtis consuming a katydid. Barro Colorado Island, Panama.

Kalka et al. 2008. Science 320: 71

## Responses of arthropods to lizard removal: rainforest in Puerto Rico



In arthropods >2 mm, predatory (spiders), parasitic (Hymenoptera), and nonpredatory (Diptera, Coleoptera, Orthoptera, and Blattaria) spp. responded to lizard removal.

Dial & Roughgarden 1995. Ecology, 76: 1821-1834





Predator exclusion:

Herbivore abundance increases (to 120-180% of original abundance) In arthropod communities, % of predators increases (compensation) In plants, damage of leaves increases (trophic cascade)



Katerina Sam Bonny Koane

#### Biological control of plants by herbivores: the success story of *Cactoblastis cactorum* controlling *Opuntia* (Australia)













Salvinia molesta and Cyrtobagous salviniae



# And now for something completely different

P. palustre S. libanotis C. moculatum B. radians P. oreoselinum R. graveolens A. archangelica 1. ostruthium O.aquatica C. dubium D. albus An. groveolens L.officinale Ang. silvestris M.athamanticum L. scoticum O. fistulosa O. lachenalii F. vulgare A. podagraria P. sativa H. lociniatum H. mantegazzianum S. silaus B. erecta P. anisum A. majus P. saxifraga S. latifolium P. crispum F. vulgaris L. latifolium D. corota C. carvi M. odorata H. sphodylium C. virosa S. carvitalia A. cynopium P. major Ap. graveolens B. rotundifolium P. austriacum C. sativum C. lappula T. japonica S. pecten-veneris A. cerefolium Ant. silvestris C. bulbosum C.temulum . aureum planum maritimum A. major S. europaea H. vulgare





#### Peucedanum palustre

## Does the host selection follows optimality rules?







Number of host species

Cephaloleia placida (1)

Tetraopes tetraophthalmus (1)

Cephaloleia belti (11) Popilia japonica (>300)

TRENDS in Plant Science

#### Herbivore host ranges are variable...

- genetically based trade-offs in performance between host species
- interspecific competition for food or enemy-free space
- increased resistance to generalist predators on some host plants
- similarity of some hosts to unsuitable hosts
- facilitated mate finding
- facilitated defence against enemies [sequestering plant metabolites]
- ability to aggregate and overwhelm plant defences

#### Why are there generalists?

- hosts are rare, unpredictable, unapparent
- small plants favouring larval grazing
- risk spreading strategies due to temporal/spatial variability in host quality
- intraspecific competition
- predator and pathogen functional/numerical response

- genetically based trade-offs in performance between host species

simultaneous specialization to multiple hosts decreases fitness on any host plant species





interspecific competition for food or enemy-free space



Fitness of herbivore X can be reduced on some plant species by competition from herbivore Y

#### increased resistance to generalist predators on some host plants



Specialists are better protected on their host plant species from generalist predators

#### Why are there generalists?

- hosts are rare, unpredictable, unapparent
- small plants favouring larval grazing
- risk spreading strategies due to temporal/spatial variability in host quality



Total supply of plant species A + B + C more abundant and less variable than for individual plant populations

#### Why are there generalists?

- intra-specific competition
- predator and pathogen functional/numerical response



optimum host selection:



#### Multiple meaning of host specificity





Host specificity mostly relatively narrow in insects and wide in vertebrates

Fig. 3.18 Monophagy and polyphagy in insect herbivores. For mesophyll-feeding leaf-hoppers and leaf-miners on British trees most species are monophagous and there are few broad polyphages (Claridge & Wilson 1981). Vertebrates and larger, leaf-chewing insects tend to show much less pronounced monophagy.



(b)

10

8

Herbivores on aliens: Cytisus scoparius







Figure 1. Average phytophage diversity per bush in the four countries: (a) total number of phytophage species; (b) specialist phyto-phage species; (c) generalist phytophage species. The bars show the standard error; ENG, England; FR, France; NZ, New Zealand; AUS, Australia.

Figure 3. (a) The average abundance of specialist phytophages per bush in England, France and New Zealand and (b) the average abundance of generalist phytophages in England, France and New Zealand.

FR

Country

NZ

ENG

160

120

80

40

0

Generalist abundance

(b)

Memmott et al. 2000, Acta Oecol. 21:23

#### "Four ways towards tropical herbivore megadiversity"



Q

#### Latitudinal gradients in host specificity: no plant standardization included



# Standardising phylogenetic diversity among food webs along latitudinal gradients

Temperate trees





#### **Tropical trees**



Novotny et al. 2006, Science 313:1115


## Higher host specificity in the tropics: a naturally standardized Curculio – Quercus system



Peguero et al., Ecology, 98(8), 2017, pp. 2180

## Oak leaf defenses:

higher in the tropics, and this gradient follows the climate.





Vertebrate herbivores: mostly generalists, but with preferences

Generalists' plant choice: minimizing time or maximizing energy



Fig. 3. The time-minimized and energy-maximized diets predicted by the linear programming model versus the observed diets are presented. demonstrating that time-minimizers are predicted to be either monocol or dicol specialists. The energy-maximizing diet explains the observed diets better. Each number represents a different species: 1. Melanopius femur-mbrum, 3. Melanopius sanguinges. 3. Clevoertix undulatus, 4. Dissosteine carolina, 5. Microtus pennsylcanicus, 6. Spermophilus columbianus, 7. Sykillagus nutalli, 8. Marnota flaubenty, 9. Antilocara americana, 10. Ocisi canadensis. 11 Odocolleus virginianus, 12. Odocolleus hemionus, 13. Cercus canadensis (or elaphus), and 14. Bison bison

# And now for something completely different

Niche structure of herbivorous communities: ecological optimization or accidents of evolution?





Herbivores on bracken (*Pteridium aquilinum*): replicated food web assemblage from different species pools

## Regional species – area curve for bracken insects



## Regional species pools vs. local communities



Figure 16.4 The relationship between local and regional species richness of herbivores feeding on bracken in different parts of the world. The "maximum" line has a slope of 1.



	Chew	Suck	Mine	Gall
Rachis		••		•
Pinna	:::::	•••	•••	••
Midribs		1	••	

## Taxonomic composition of replicated herbivore communities on bracken







Noctuidae, Tortricidae, Pyralidae, Psychidae, Cosmopterigidae, Tineidae, Geometridae, Lyonettidae, Limacodidae, Gelechiidae, Lymantriidae, Lasiocampidae, Arctiidae





UNITED STATES	Chew		Suck					Mine	Gall
Seeds							-		
Flowers						Τ			
Foliage	•					T			
Stems								•	
Roots									

Biogeographical comparison of the arthropod herbivore communities associated with *Lepidium draba* in its native, expanded and introduced ranges

Michael G. Cripps<sup>1</sup>\*, Mark Schwarzländer<sup>1</sup>, Jessica L. McKenney<sup>1</sup>, Hariet L. Hinz<sup>2</sup> and William J. Price<sup>3</sup>









### Herbivore guild structure:

- is it predictable?
- is there between-guild compensation?

#### beetles and aphids

highlighted just to illustrate general point of variability in guild composition among host tree species

pare 22-4. Goal and suscensin generation the herbivirous at produces 1. Microlaphicagenze, 1R, Vanchardingenze, 1R, Vanchard, 1R, V



Guilds differ in their host specialization

## Specialized guilds tend to be species poor





Island biogeography: trees are "habitat islands"

Number of resident species

 $S_{\rm CS}^{*}$ 

 $S^*_{\mathrm{DS}}$ 

Close, small

Distant, large

Distant, small

Small

Large

 $S^*_{\mathsf{CL}}$ 

 $S_{\mathsf{DL}}^{*}$ 

Wilson and Simberloff (1970): experimental tests of the theory, monitoring arthropod immigration and extinction after complete defaunation of small mangrove islands offshore Florida



Experimental test of the effect of island area on species richness



## Assembly of local communities from regional species pool





### Species richness of herbivore communities: determined by plant abundance



## Plant evolution in real-time: changes after insect exclusion for 5 years control plot - insects present insects excluded



2010



Oenothera biennis



Lower resistance to seed-eating insects

2009

0.97

2007

2008

Higher competitive ability (with Taraxacum officinale)

## Tannins (Oenothein A): decreased in fruits in the absence of insects



Lifetime seed production: correlated with oenothein but only when insects are present

Early flowering: advantageous response in the absence of insects

Agrawal et al. SCIENCE VOL 338 5 OCTOBER 2012

# THE END

