

# Parasites and biological invasions: from individuals to interaction networks

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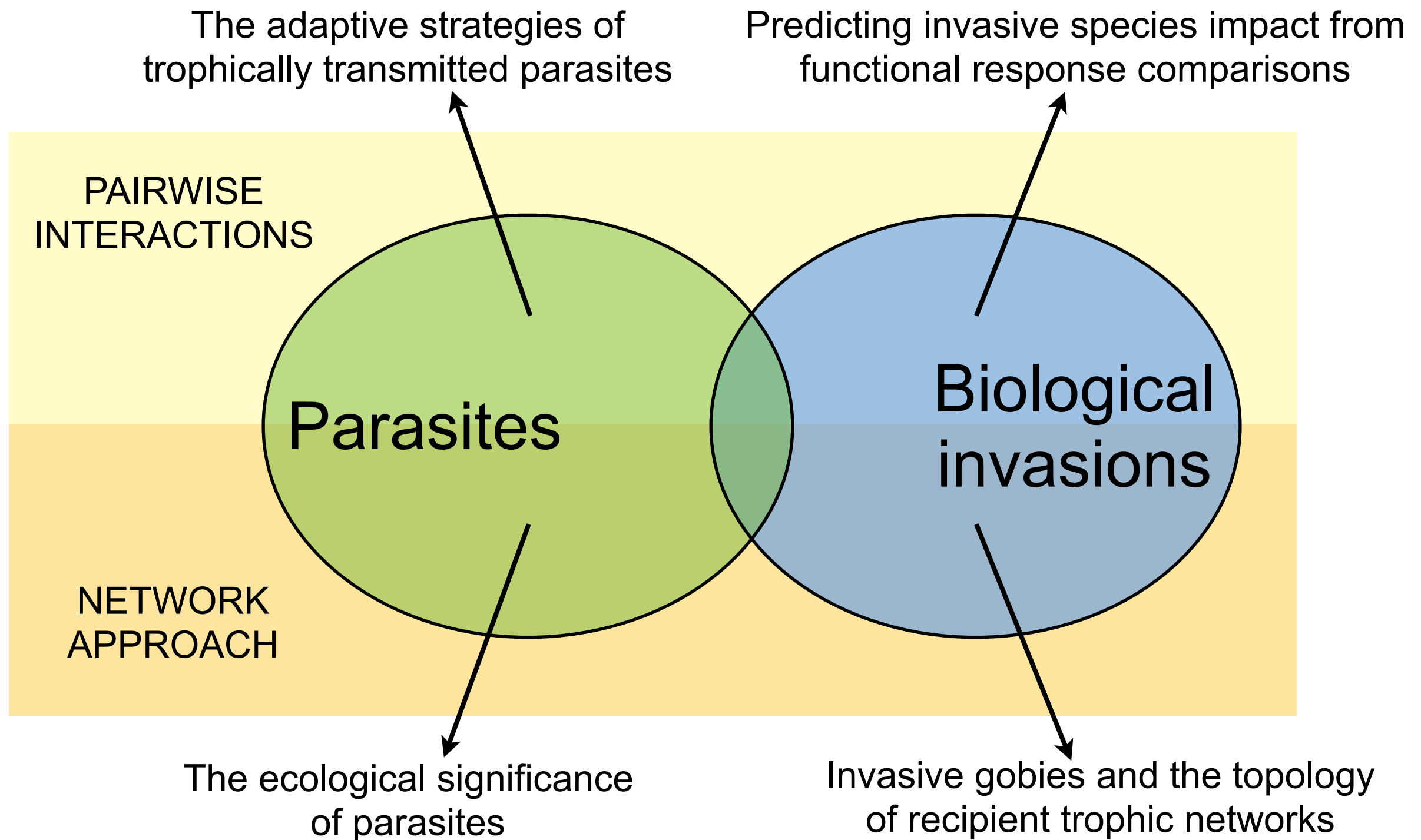
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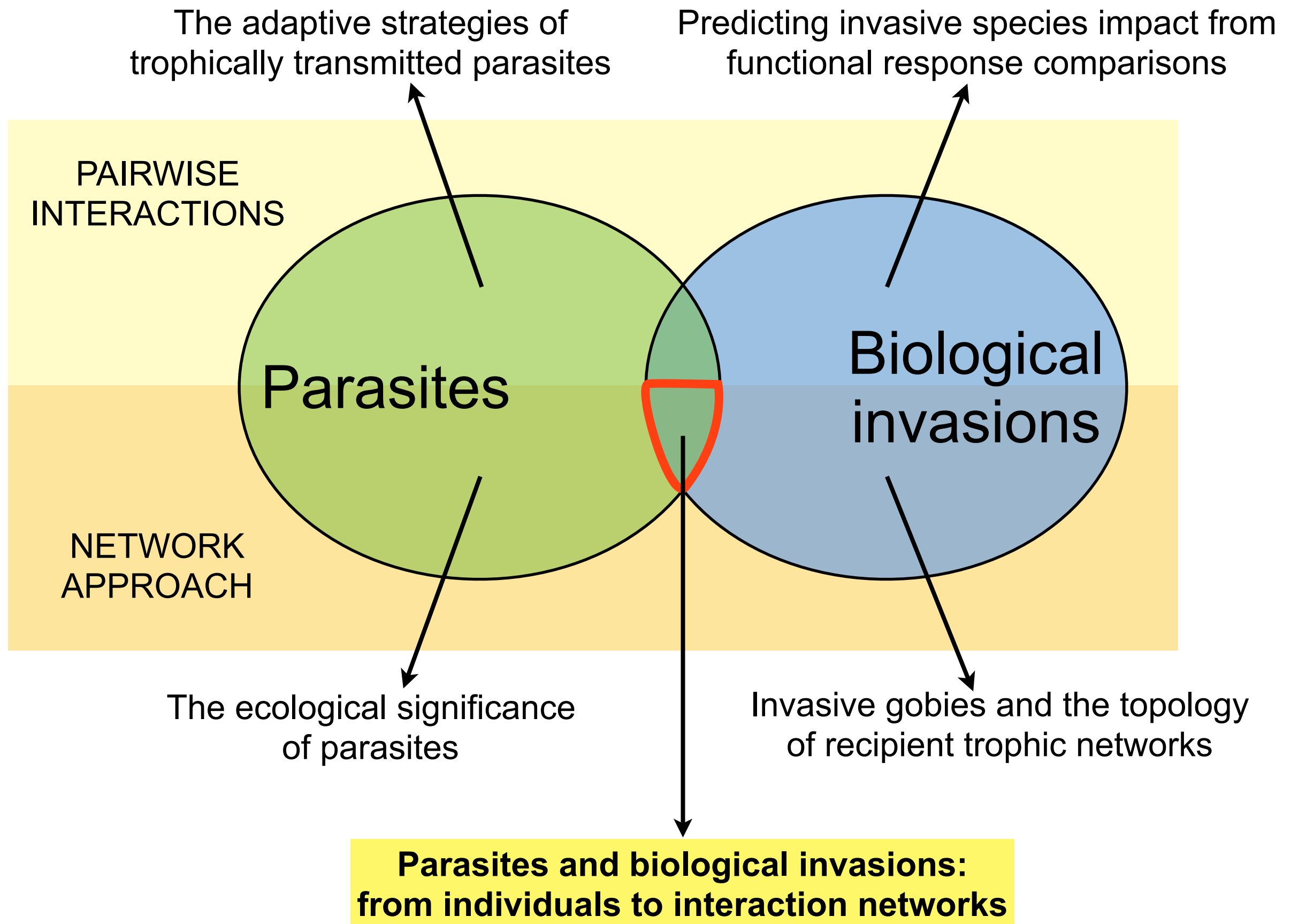
Journée thématique «Réseaux, Invasions et Emergences»

11 mai 2017, CBGP, Montpellier

# Ongoing projects



# Ongoing projects



# Outline

- The framework

- The diversity of parasite strategies

- Parasites in invasion ecology

  - The enemy release hypothesis

  - Parasites as alien species

  - Processes involving parasites

- Parasites in trophic networks

  - The network approach in ecology

    - Some topological descriptors

    - Linking network topology and community properties

  - Including parasites in trophic networks

  - Parasite - induced changes in topology

  - Parasite - induced changes in community properties

- Parasites in invaded networks

  - Impact of introduced parasites on food-web structure

  - Linking network structure and invasibility

  - How invader-induced changes in topology affect parasites

# Outline

## The framework

The diversity of parasite strategies

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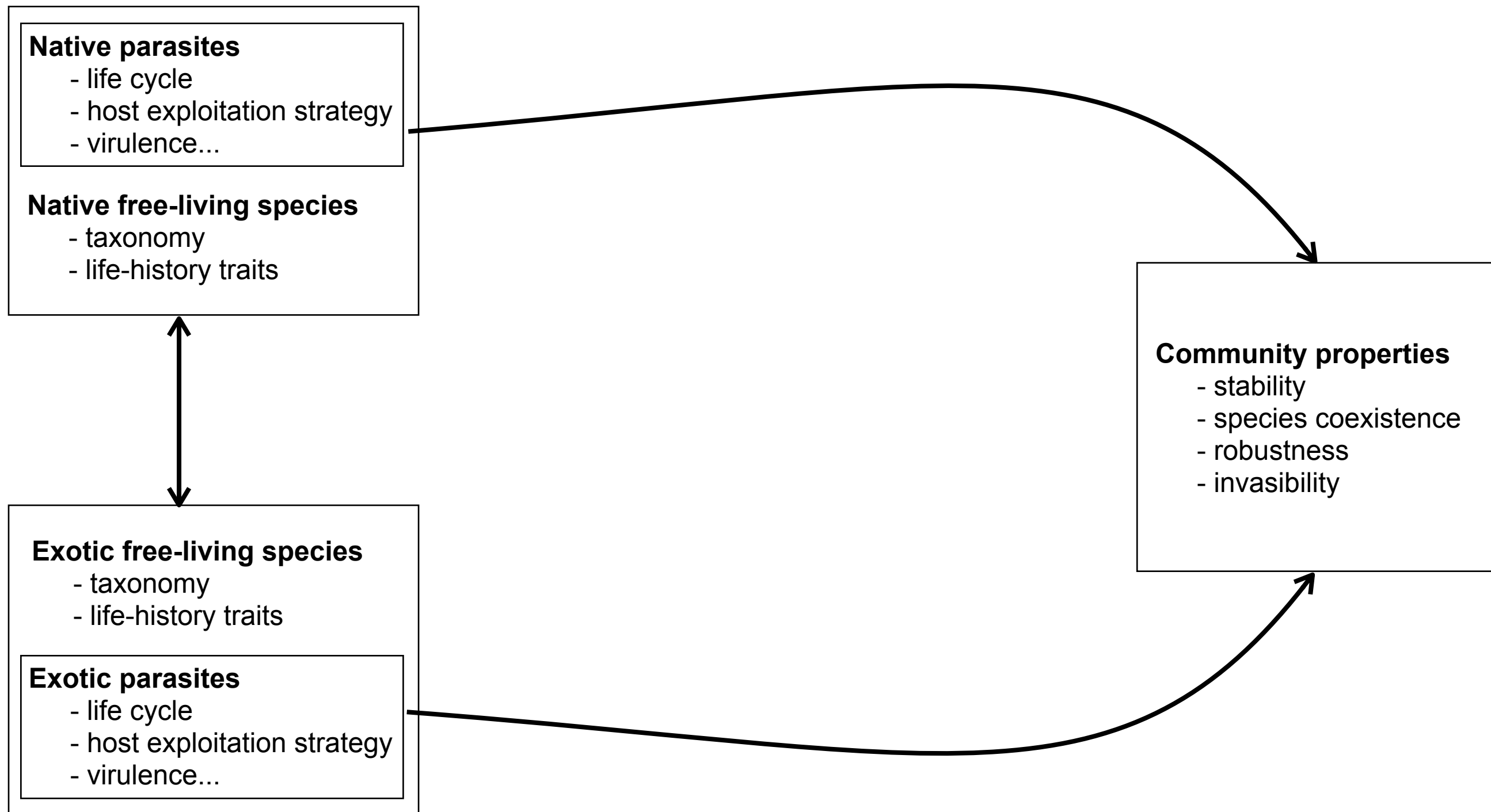
Parasites in invaded networks

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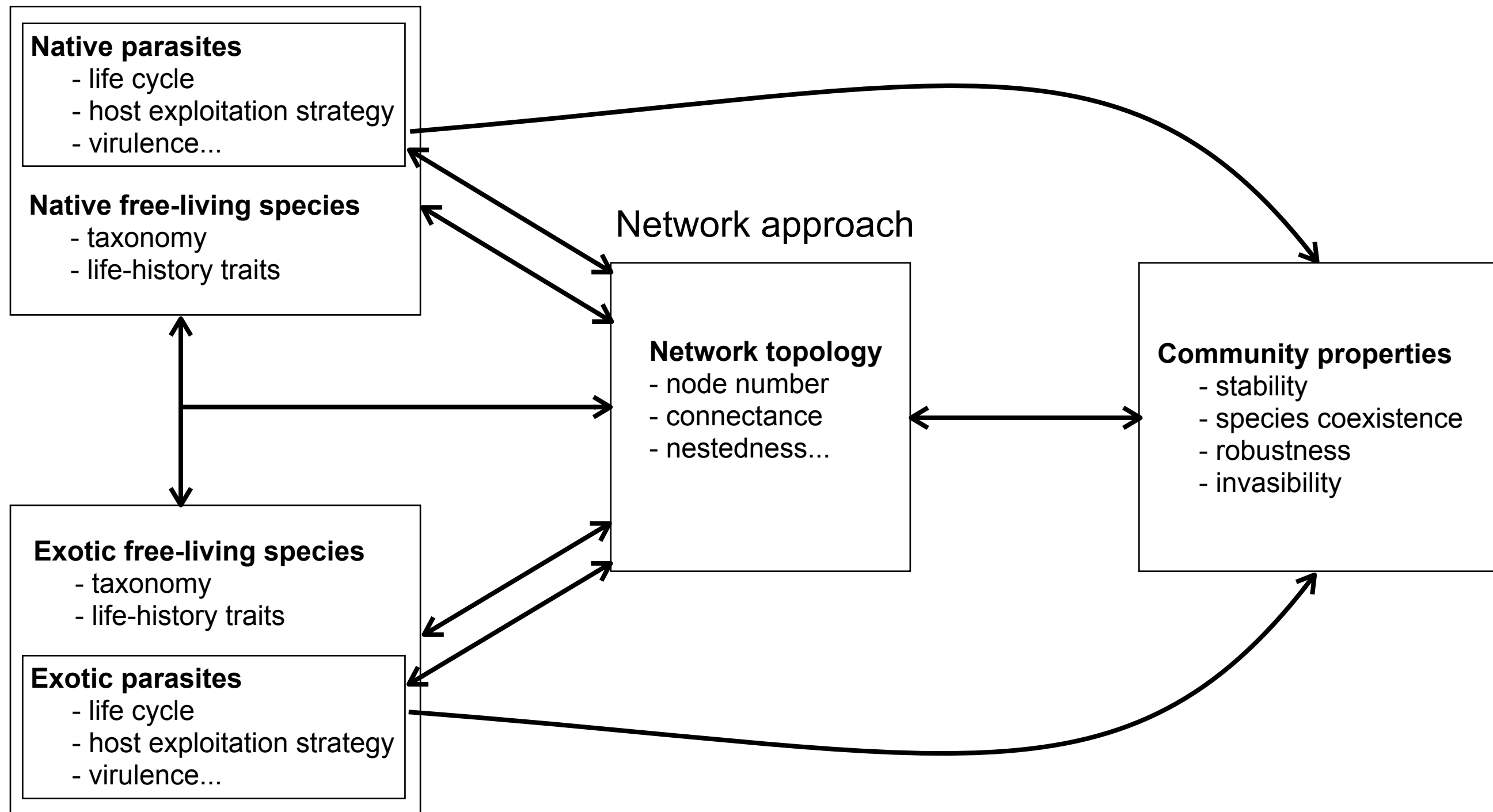
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# The framework



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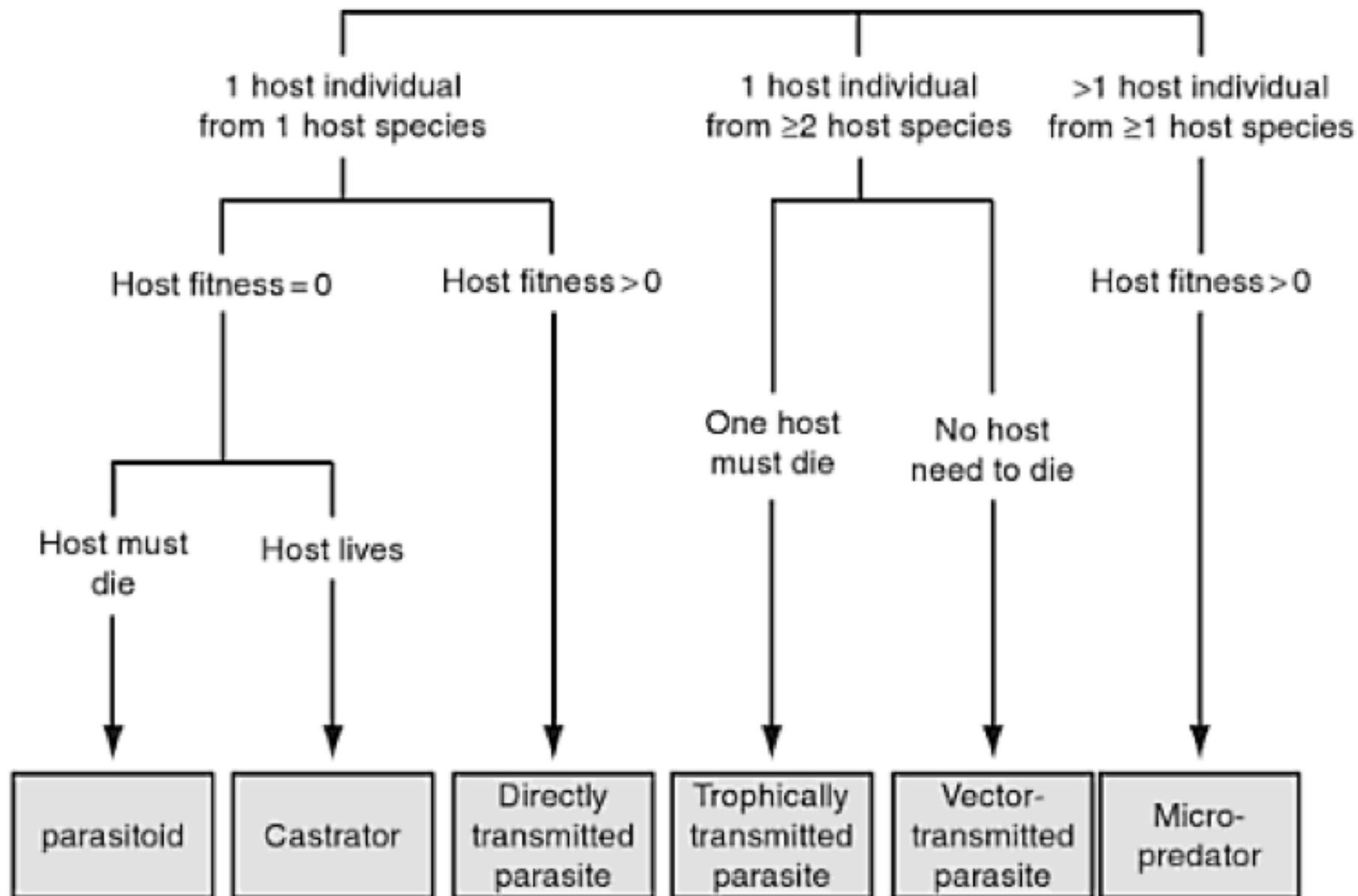
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# The diversity of parasite strategies



**FIGURE 1.1** Classification tree of the six parasitic strategies considered here, and encompassing the vast majority of known parasite taxa. The first division is based on the number of hosts used, both in terms of species and individuals, by one full parasite generation; subsequent divisions are based on fitness impact on hosts.

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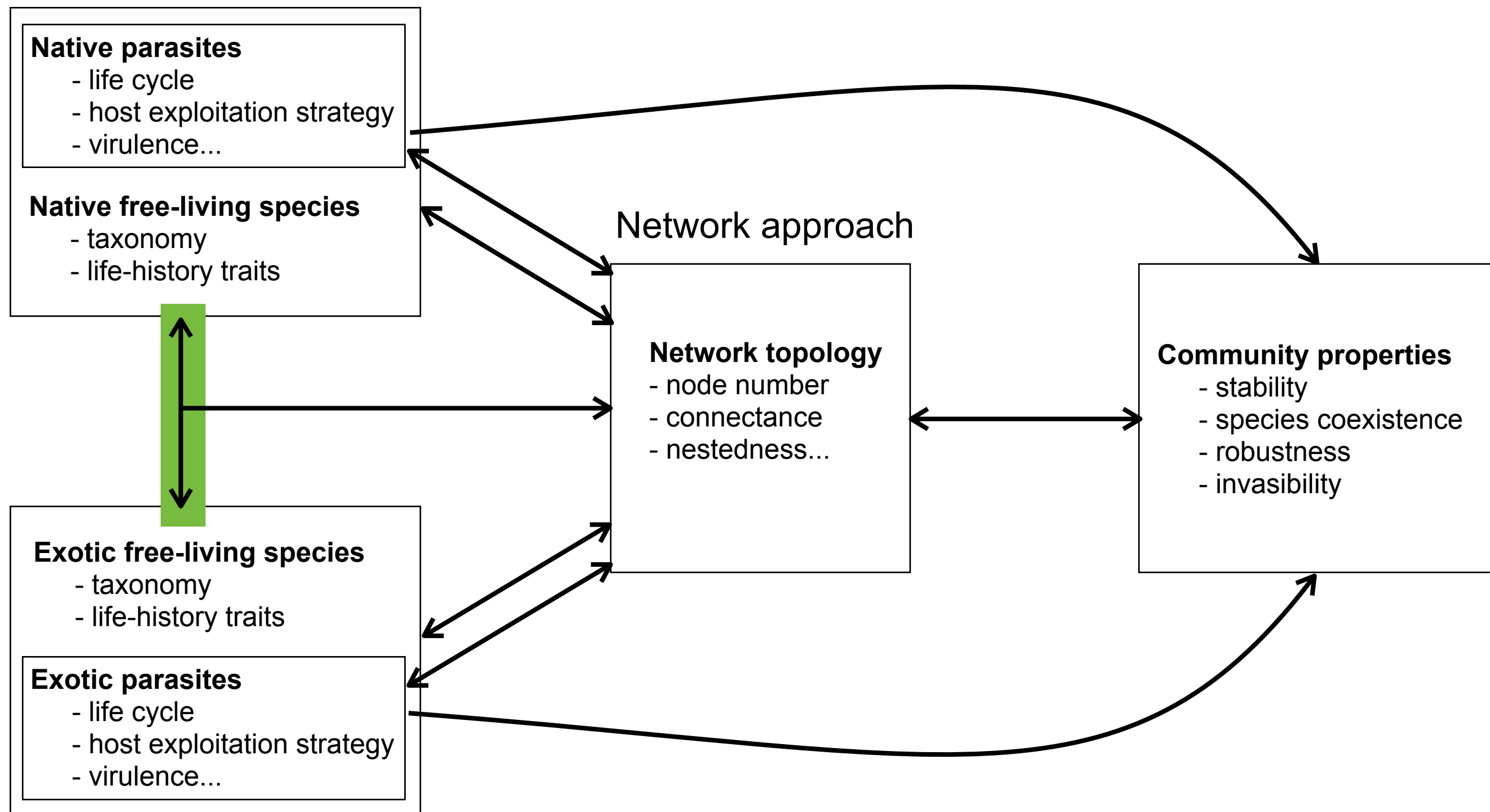
Parasites in invaded networks

Impact of introduced parasites on food-web structure

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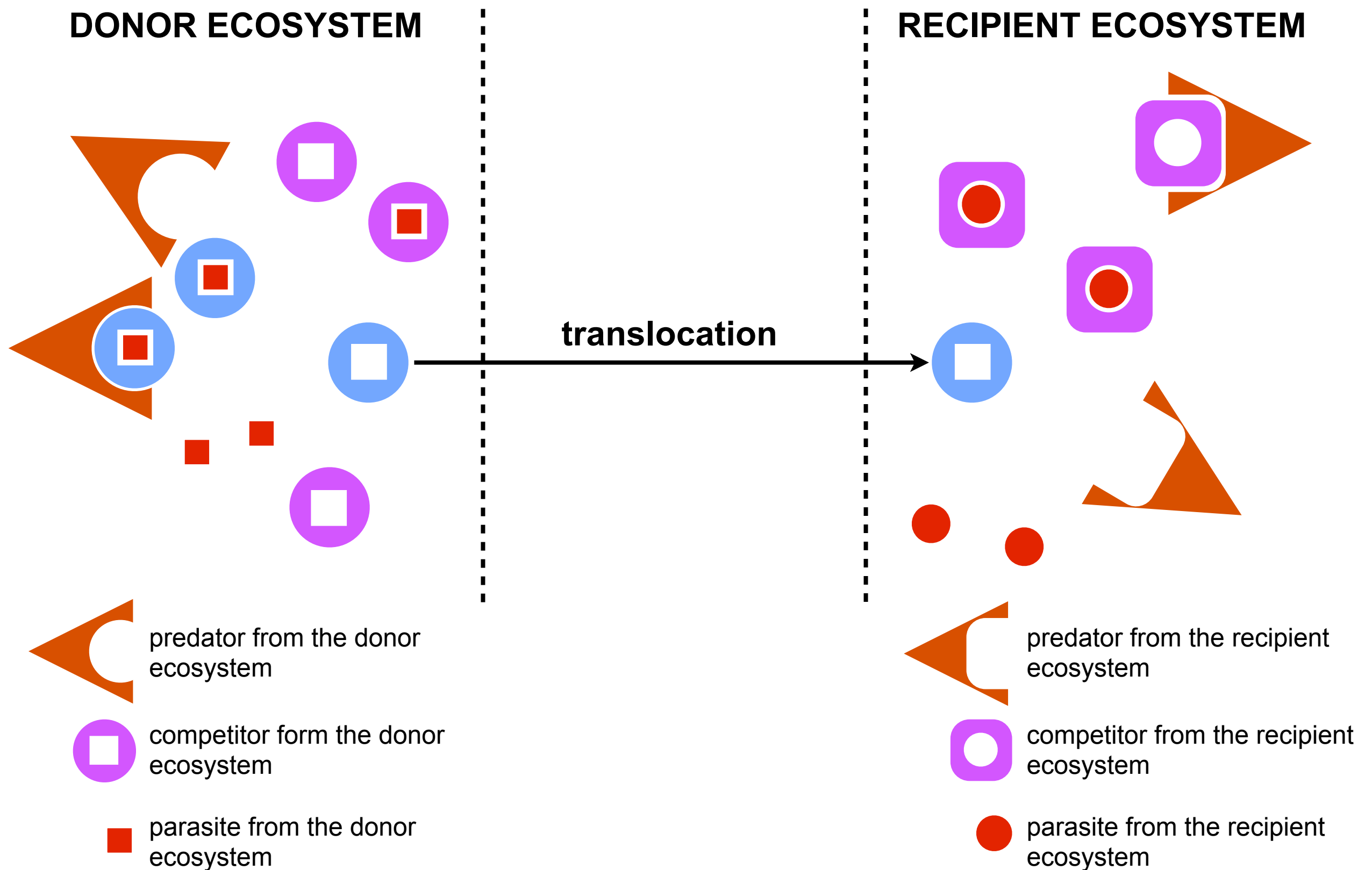
How invader-induced changes in topology affect parasites

# Parasites in invasion ecology



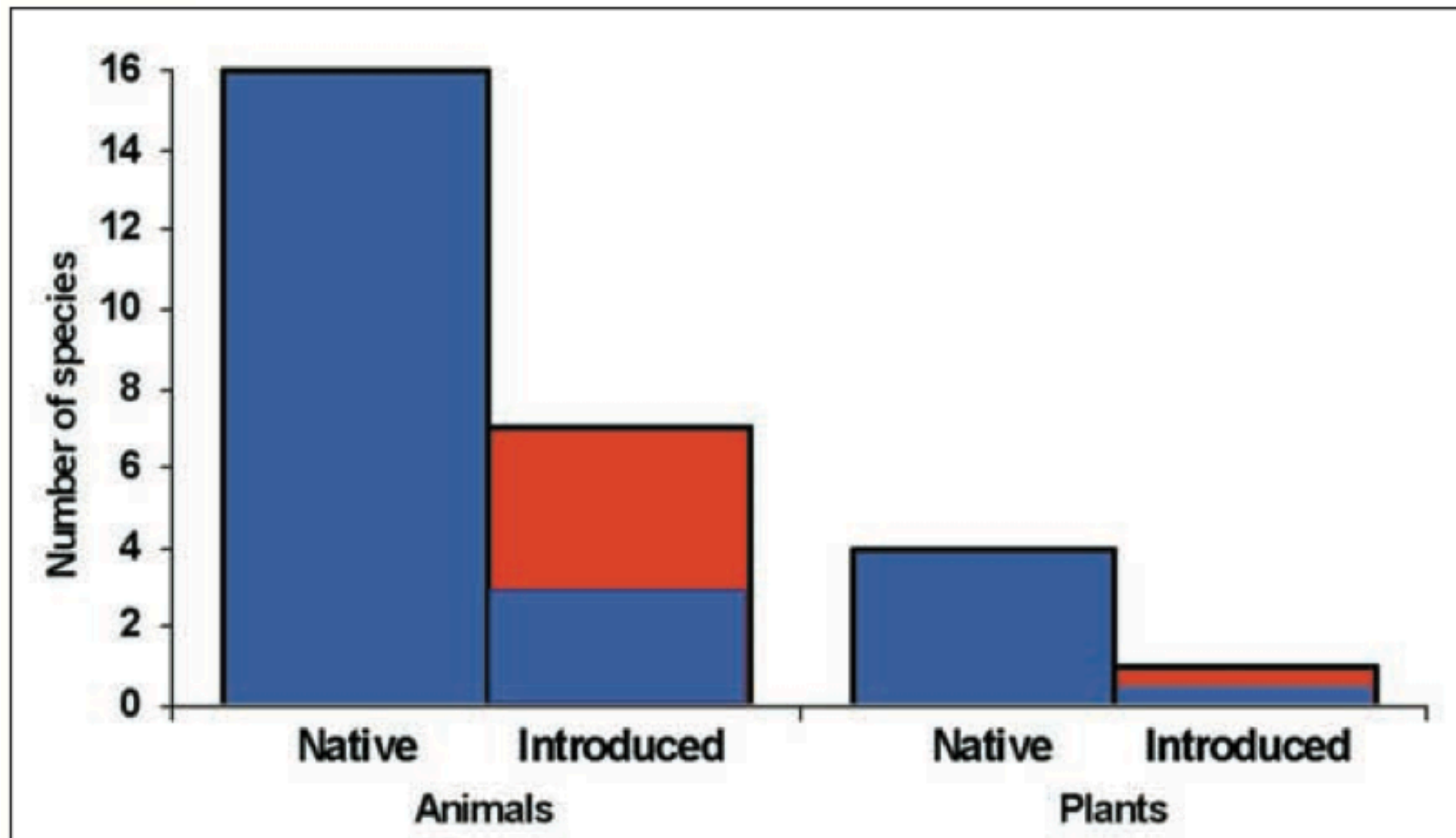
# Parasites in invasion ecology

## The enemy release hypothesis (Keane and Crawley 2002. Trends Ecol Evol 17)



# Parasites in invasion ecology

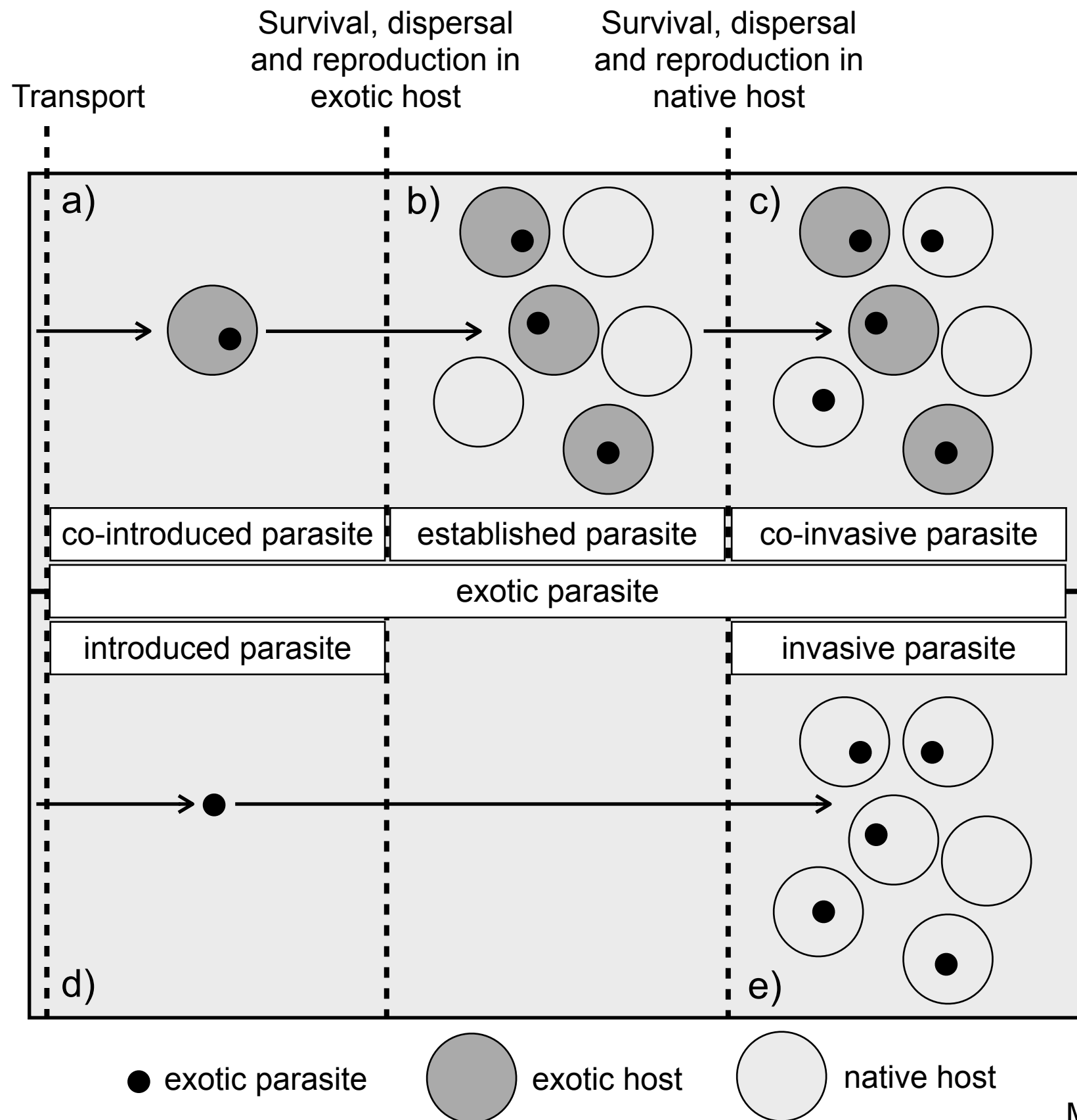
## The enemy release hypothesis (Keane and Crawley 2002. Trends Ecol Evol 17)



**Figure 2.** Release from parasites as average number of parasites in native and introduced animals and average number of pathogens on native and introduced plants. Blue bars indicate parasites/pathogens from the invader's native region and red bars indicate novel parasites/ pathogens that were accumulated in the introduced region. Data are from Mitchell and Power (2003) and Torchin et al. (2003).

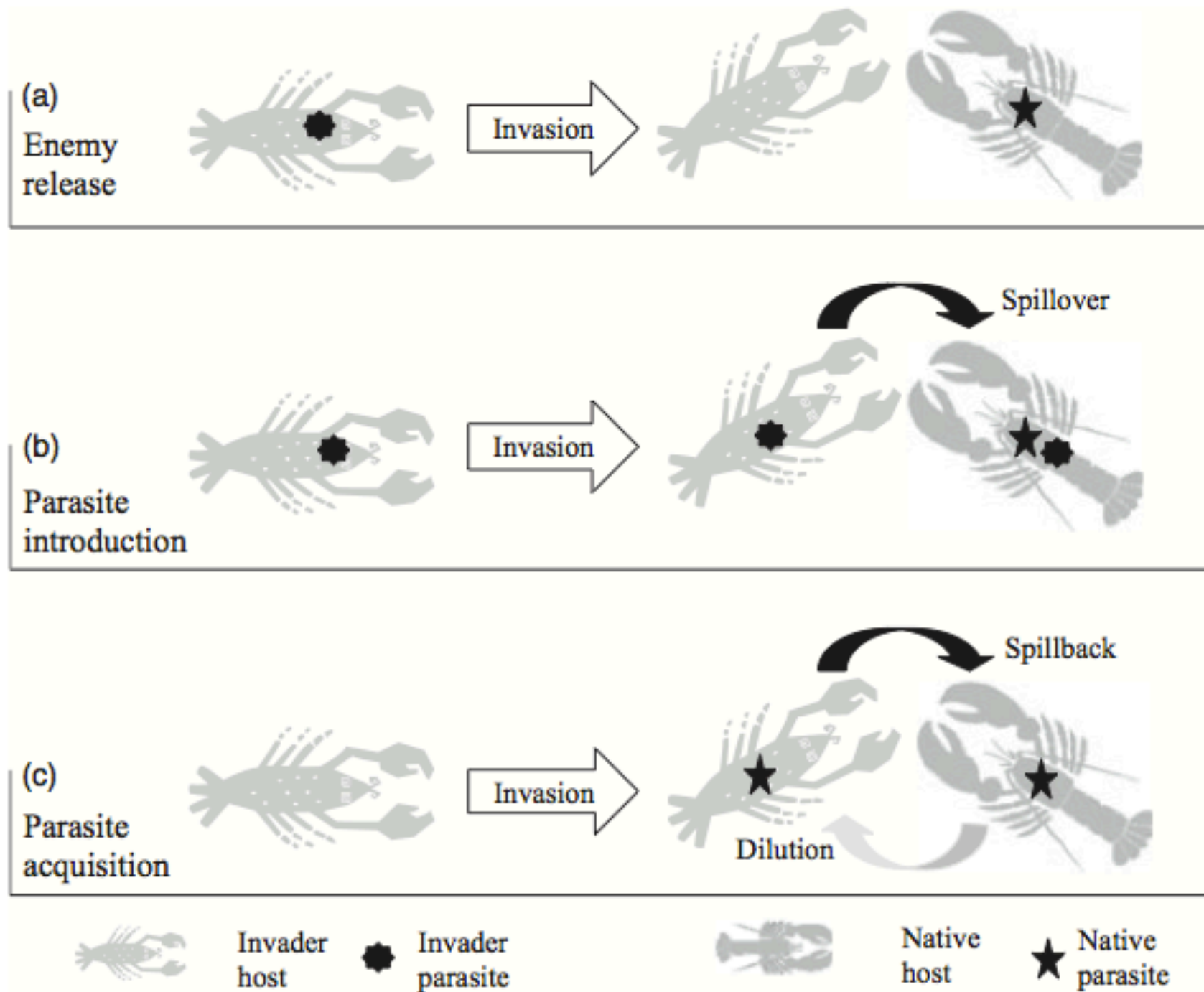
# Parasites in invasion ecology

## Parasites as alien species



# Parasites in invasion ecology

## Processes involving parasites



**Fig. 1.** The fate of parasites in the course of an invasion. Many invaders fail to establish. For invaders that succeed, the main outcomes for parasites are illustrated. (a) Enemy release; loss of parasites during the invasion process may benefit the invader. Parasites may be lost through the effects of sub-sampling or through selective pressures experienced during translocation or establishment. (b) Parasite introduction; parasites introduced with the invader may spillover to infect species in the invaded habitat. (c) Parasite acquisition; an invader may acquire parasites in the new habitat. If the invader is a less competent host, this may dilute the impact of the parasite (grey arrow). However, if the invader is a more competent host, spillback of parasites to native hosts may occur (black arrow).



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- Impact of introduced parasites on food-web structure

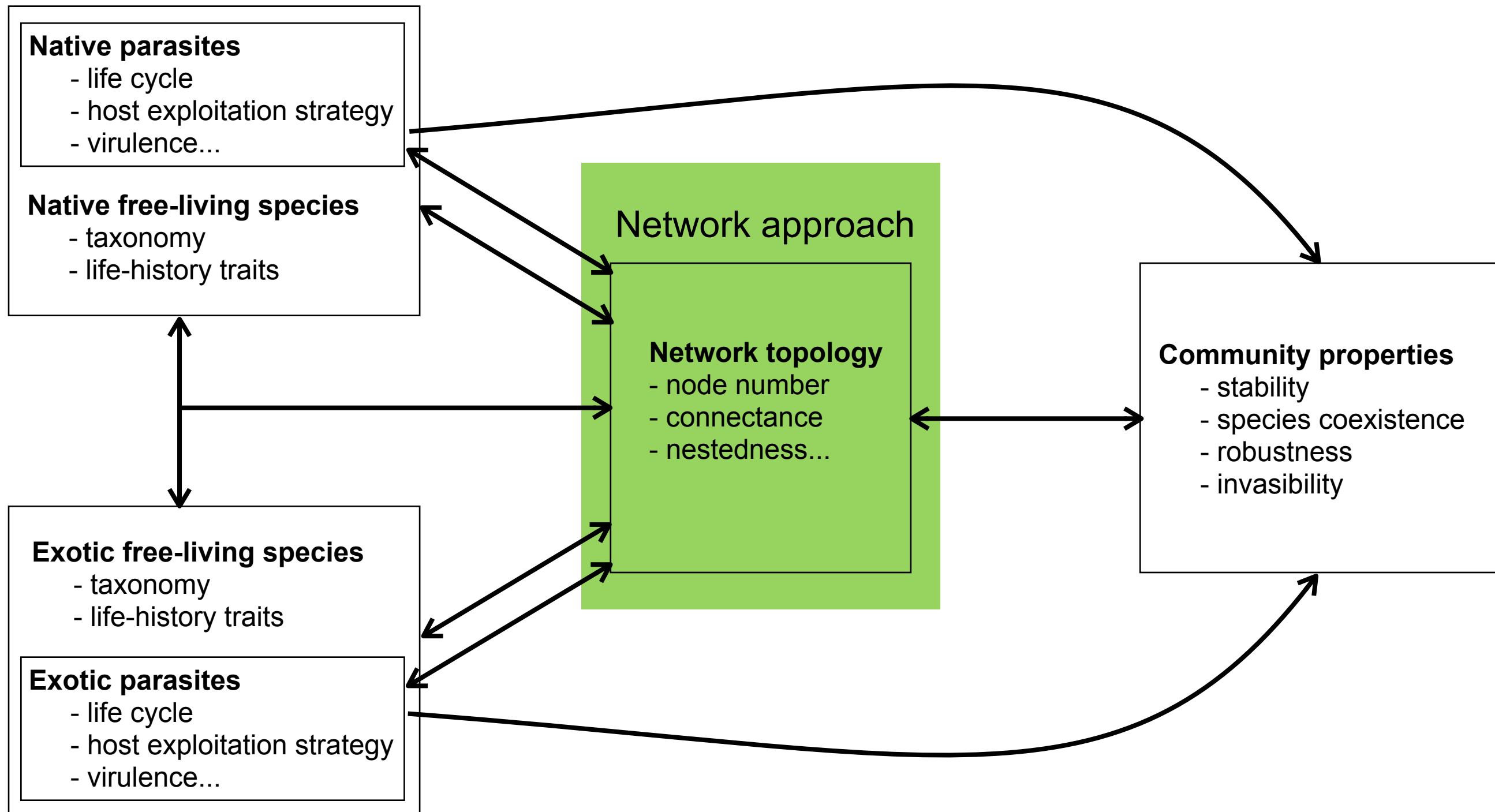
- Linking network structure and invasibility

- How invader-induced changes in topology affect parasites



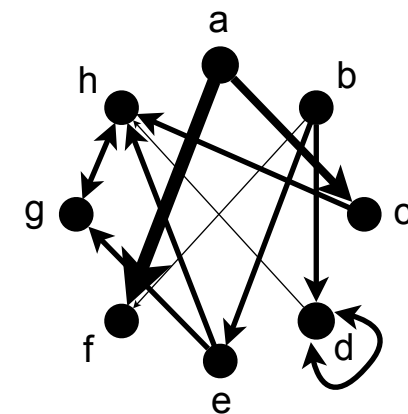
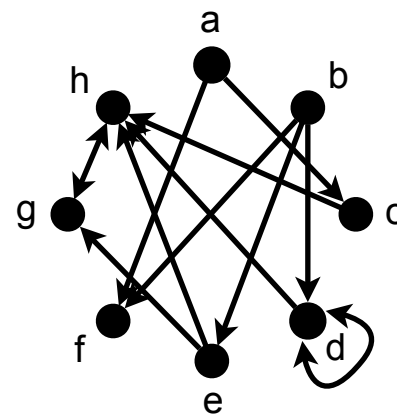
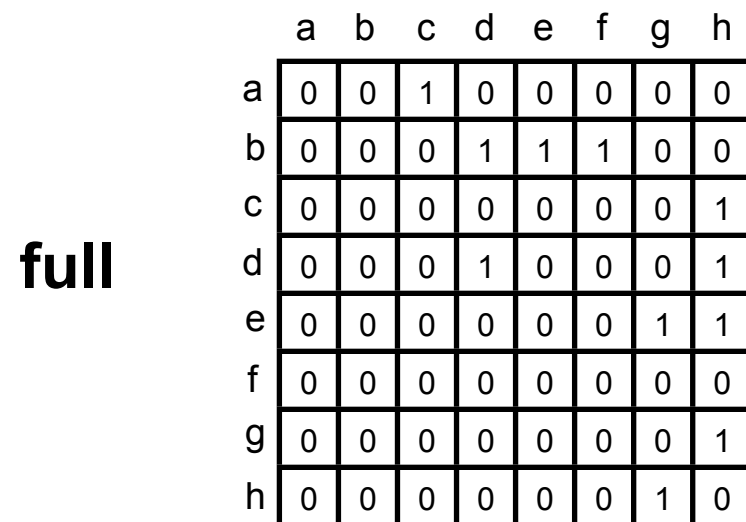
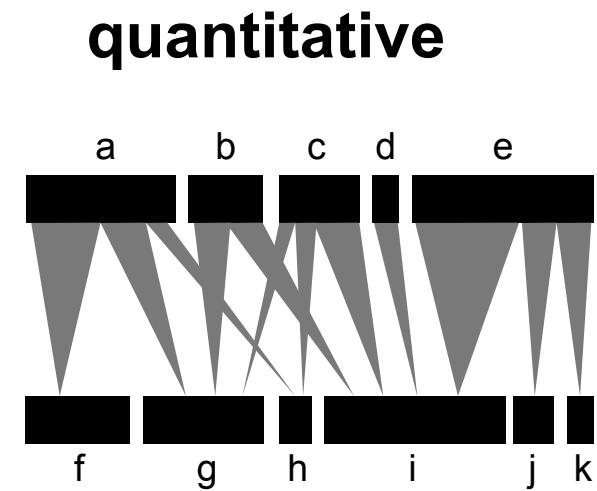
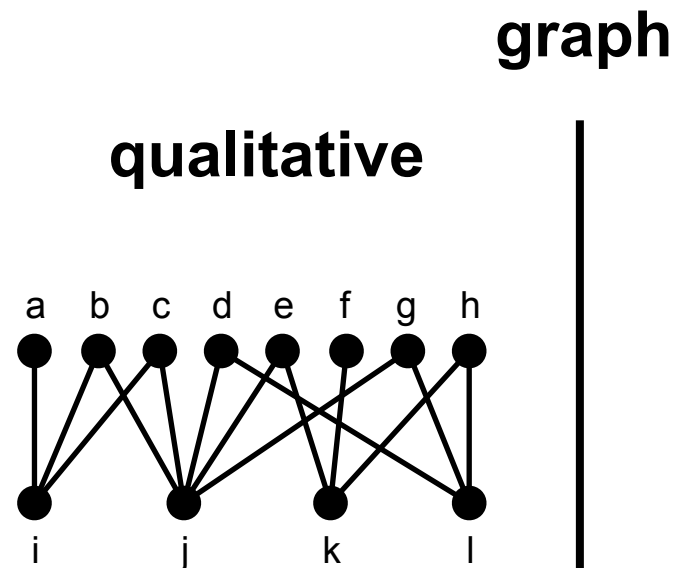
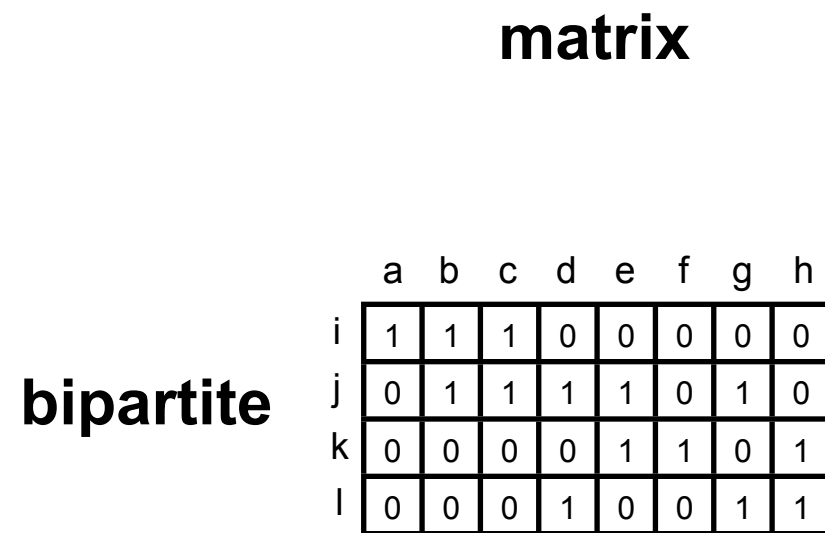
# Parasites in trophic networks

## The network approach in ecology



# Parasites in trophic networks

## The network approach in ecology



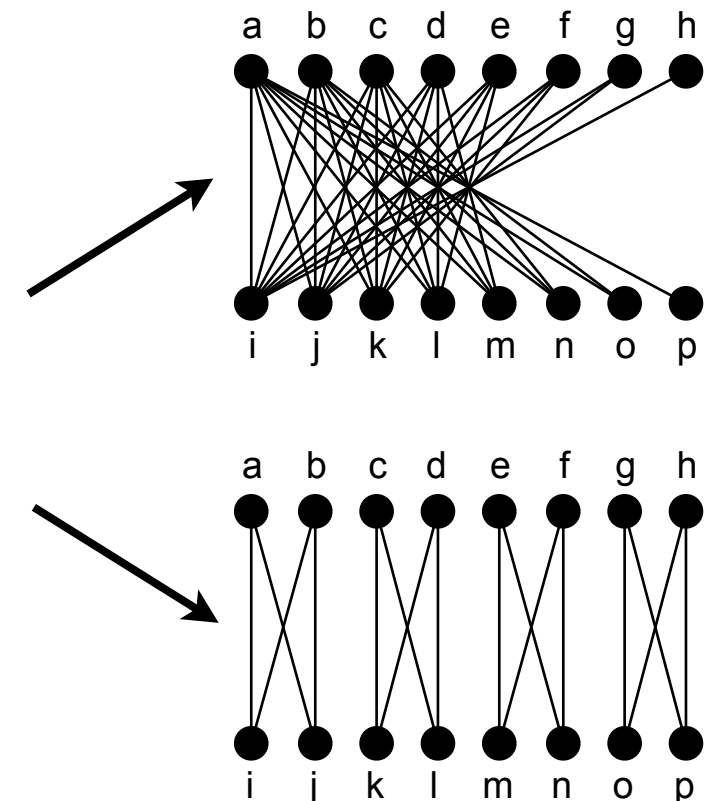
# Parasites in trophic networks

## The network approach in ecology

### Some topological descriptors:

Metric	Definition
Richness	Number of nodes
Connectance	Proportion of possible links that are realized
Link density	Mean number of links per node
Generality	Mean number of prey or host per predator or parasite species
Vulnerability	Mean number of predator or parasite per prey or host species
Omnivory	Proportion of taxa that feed on more than one trophic level
Chain length	Total number of trophic levels
Nestedness	Nonrandom pattern of link distribution where specialist taxa interact with a proper subset of the group of taxa with which generalists interact
Modularity	Nonrandom pattern of link distribution where taxa form groups of highly connected taxa (i.e. modules) with more links among themselves than with the taxa of other groups

For more details on the metrics, their quantitative versions and their calculation, see [Bersier et al. \(2002\)](#), [Bascompte et al. \(2003\)](#), [Olesen et al. \(2007\)](#) and [Fortuna et al. \(2010\)](#).





# Parasites in trophic networks

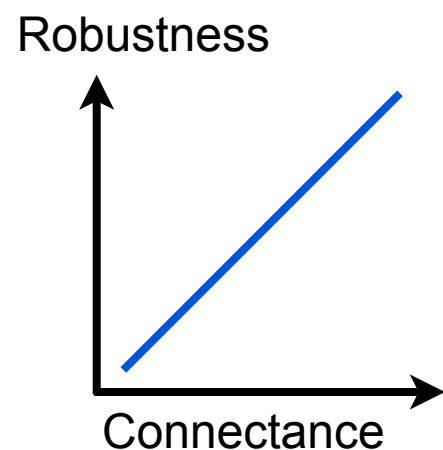
## The network approach in ecology

### Linking network topology and community properties

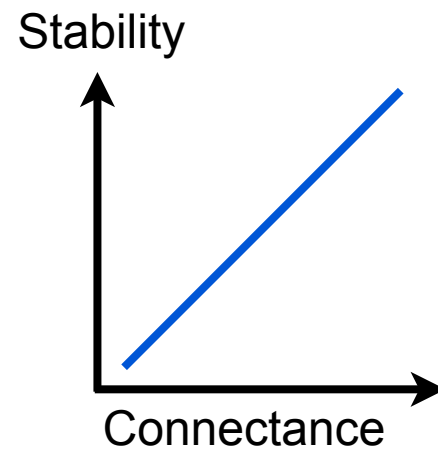
#### Connectance and stability / robustness

Dunne et al. (2002) Ecol Lett 5

Tylianakis et al. (2010) Biol Conserv 143

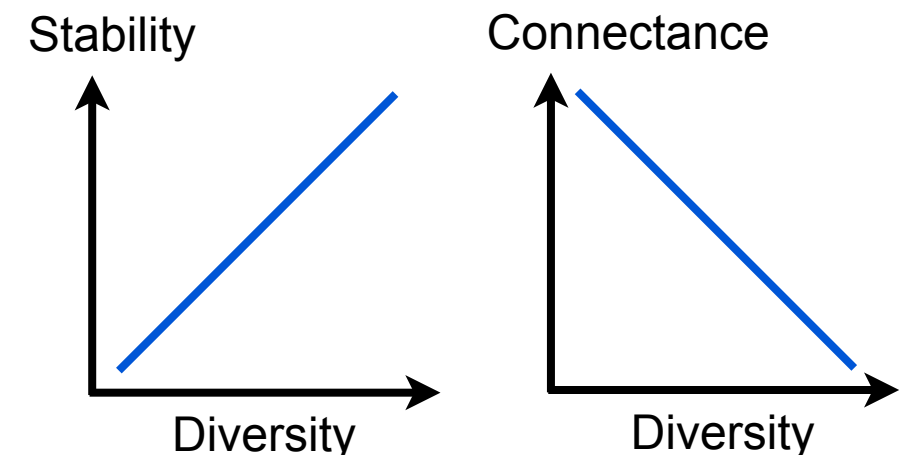
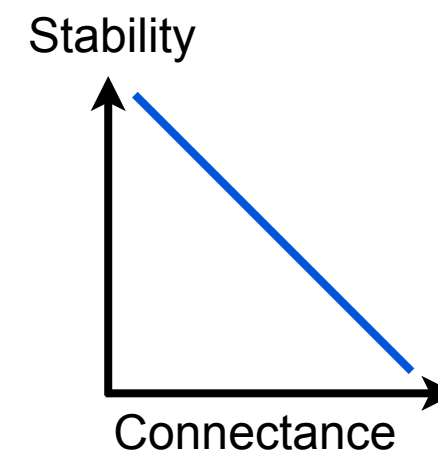


*buffer in the response of predators to fluctuating prey abundances*



*increased generalism which stabilizes the rate of ecosystem processes*

Thébault and Fontaine (2010) Science 80



*greater negative effect of apparent competition in highly connected webs*

# Parasites in trophic networks

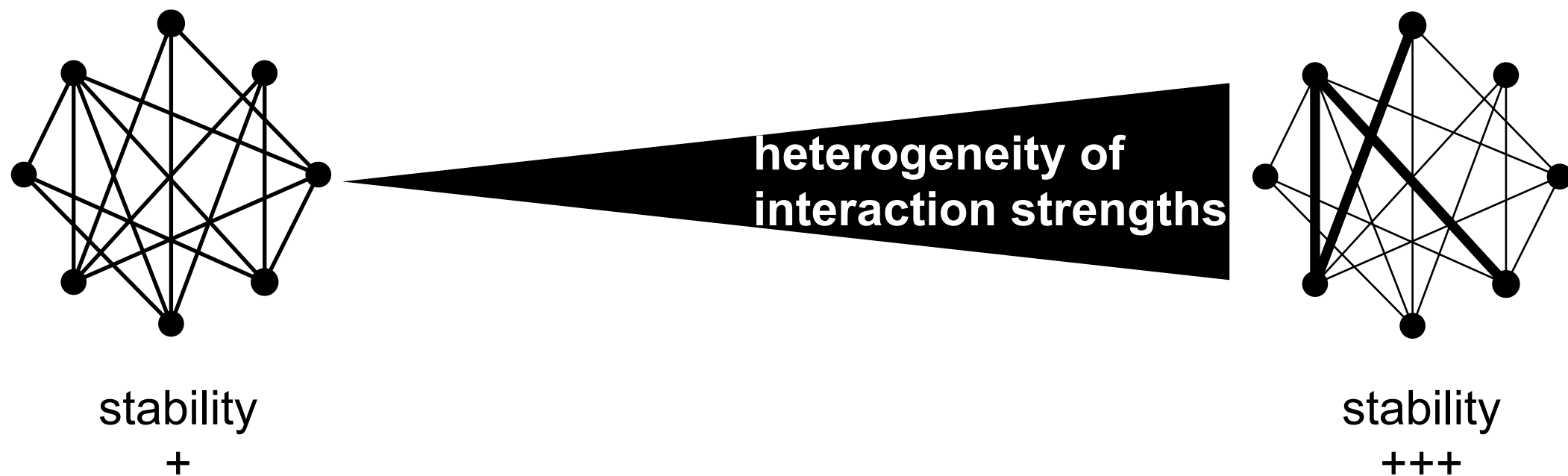
## The network approach in ecology

### Linking network topology and community properties

#### Distribution of interaction strengths and stability

McCann et al. (1998) Nature 395

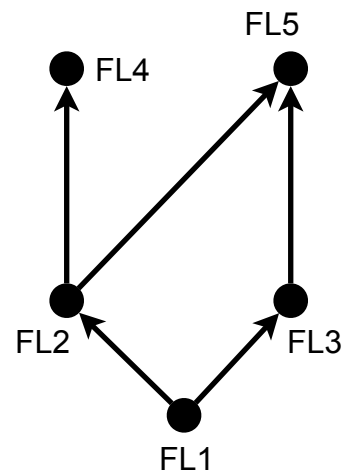
Rooney and McCann (2012) Trends Ecol Evol 27



# Parasites in trophic networks

## Including parasites in trophic networks

**trophic network**

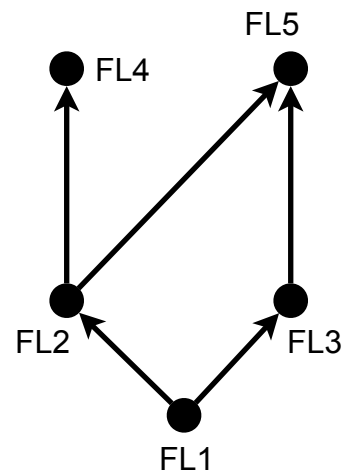


	FL1	FL2	FL3	FL4	FL5
FL1	0	1	1	0	0
FL2	0	0	0	1	1
FL3	0	0	0	0	1
FL4	0	0	0	0	0
FL5	0	0	0	0	0

# Parasites in trophic networks

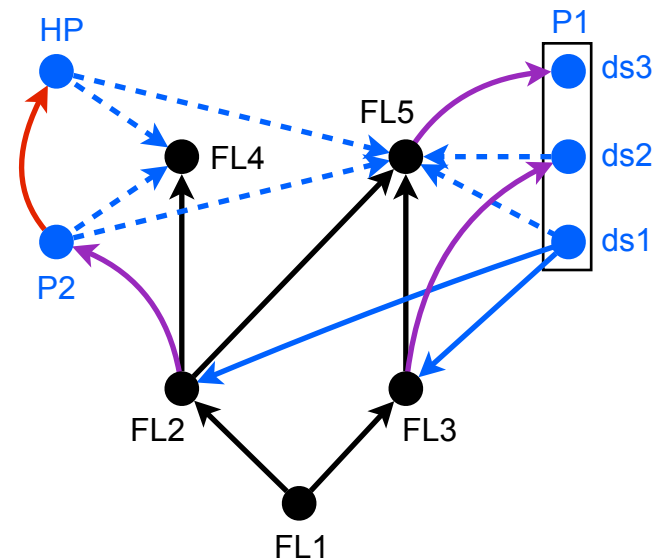
## Including parasites in trophic networks

trophic network



	FL1	FL2	FL3	FL4	FL5
FL1	0	1	1	0	0
FL2	0	0	0	1	1
FL3	0	0	0	0	1
FL4	0	0	0	0	0
FL5	0	0	0	0	0

'full' trophic network or 'infectious' network



- Predator - Prey links
- Parasite - Host links
- Predator - Parasite links
- - direct predation
- - - - concomitant predation
- Parasite - Parasite links

predator - prey  
subweb

predator - parasite  
subweb

	FL1	FL2	FL3	FL4	FL5	P1	P2	HP
FL1	0	1	1	0	0	0	0	0
FL2	0	0	0	1	1	0	1	0
FL3	0	0	0	0	1	1	0	0
FL4	0	0	0	0	0	0	0	0
FL5	0	0	0	0	0	1	0	0
P1	0	1	1	0	1	0	0	0
P2	0	0	0	1	1	0	0	1
HP	0	0	0	1	1	0	0	0

parasite - host  
subweb

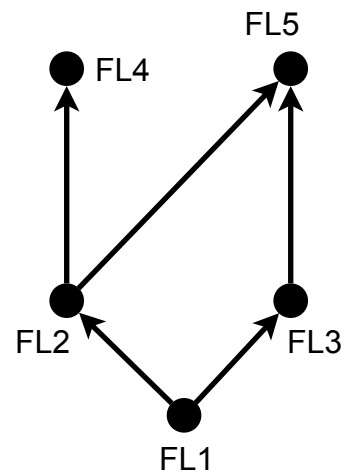
parasite - parasite  
subweb



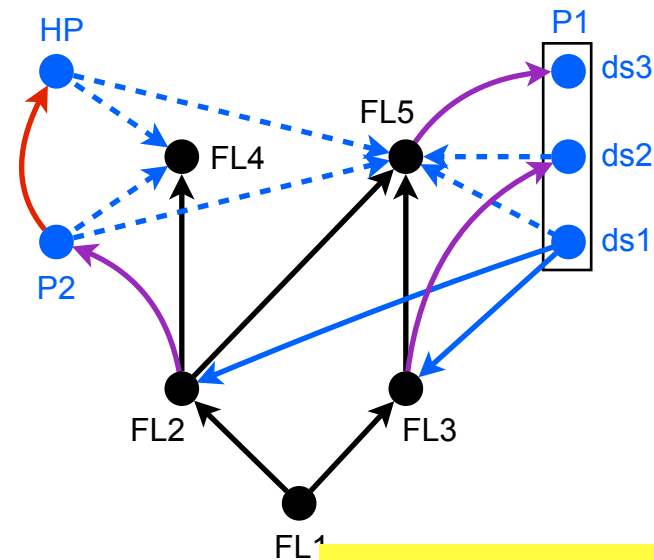
# Parasites in trophic networks

## Including parasites in trophic networks

### trophic network



### 'full' trophic network or 'infectious' network



- Predator - Prey links
- Parasite - Host links
- Predator - Parasite links
- - direct predation
- - - - concomitant predation
- Parasite - Parasite links

the node resolution issue:

nodes = taxonomic species

	FL1	FL2	FL3	FL4	FL5	P1	P2	HP
FL1	0	1	1	0	0	0	0	0
FL2	0	0	0	1	1	0	1	0
FL3	0	0	0	0	1	1	0	0
FL4	0	0	0	0	0	0	0	0
FL5	0	0	0	0	0	1	0	0
P1	0	1	1	0	1	0	0	0
P2	0	0	0	1	1	0	0	1
HP	0	0	0	1	1	0	0	0

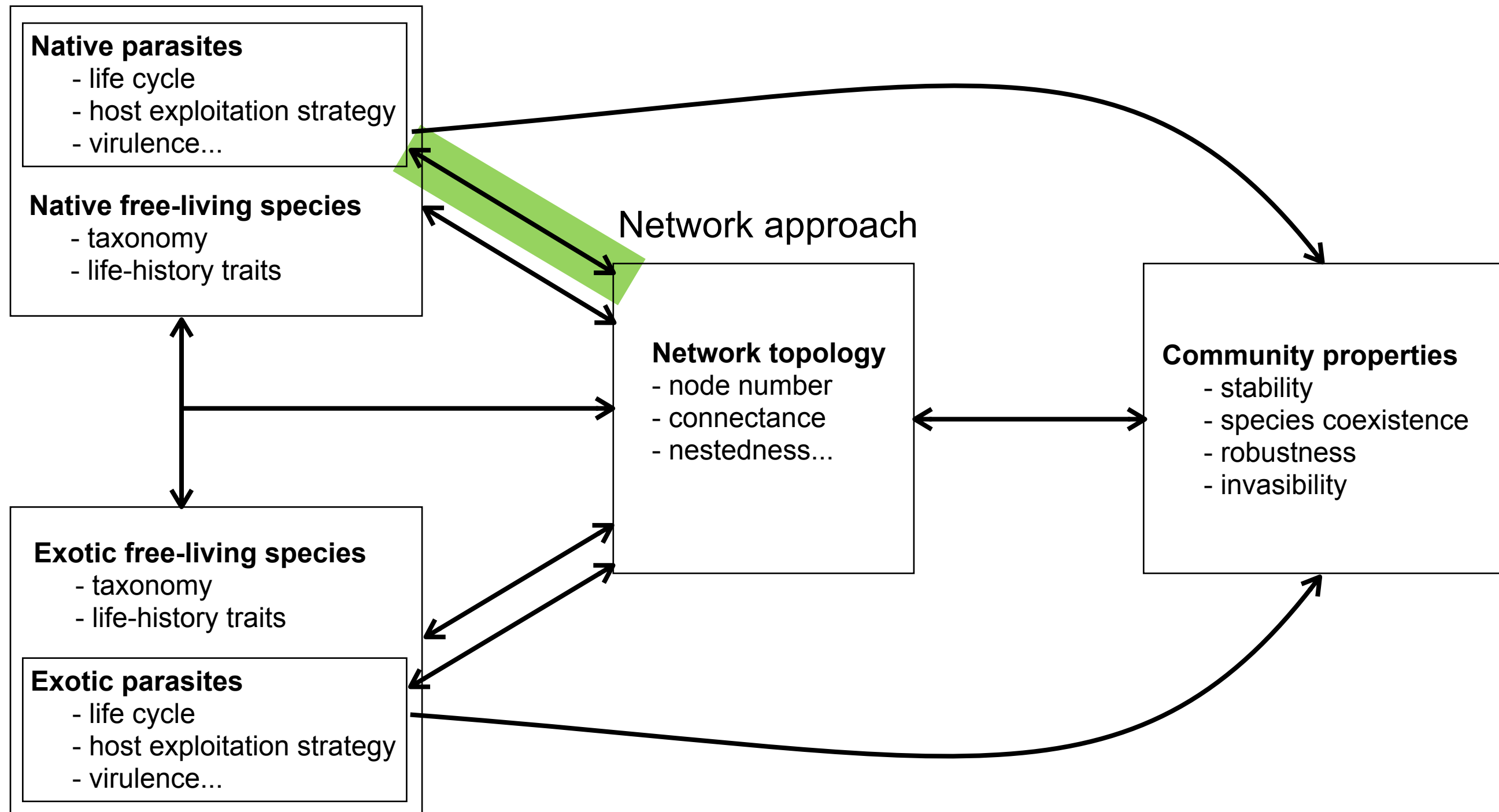
nodes = developmental stages

	FL1	FL2	FL3	FL4	FL5	ds1	ds2	ds3	P2	HP
FL1	0	1	1	0	0	0	0	0	0	0
FL2	0	0	0	1	1	0	0	0	1	0
FL3	0	0	0	0	1	0	1	0	0	0
FL4	0	0	0	0	0	0	0	0	0	0
FL5	0	0	0	0	0	0	0	1	0	0
ds1	0	1	1	0	1	0	0	0	0	0
ds2	0	0	0	0	1	0	0	0	0	0
ds3	0	0	0	0	0	0	0	0	0	0
P2	0	0	0	1	1	0	0	0	0	1
HP	0	0	0	1	1	0	0	0	0	0

	FL1	FL2	FL3	FL4	FL5
FL1	0	1	1	0	0
FL2	0	0	0	1	1
FL3	0	0	0	0	1
FL4	0	0	0	0	0
FL5	0	0	0	0	0

# Parasites in trophic networks

## Parasite - induced changes in topology



# Parasites in trophic networks

## Parasite - induced changes in topology

Name	Location	References
Loch Leven	United Kingdom	Huxham et al. (1995)
Ythan Estuary	United Kingdom	Huxham et al. (1995)
Broom fauna at Silwood Park	United Kingdom	Memmott et al. (2000)
Otago Harbour	New Zealand	Thompson et al. (2005) and Mouritsen et al. (2011)
Carpinteria Salt Marsh	USA, California	Lafferty et al. (2006), Kuris et al. (2008) and Hechinger et al. (2011)
Estero de Punta Banda	Mexico	Kuris et al. (2008) and Hechinger et al. (2011)
Bahía Falsa	Mexico	Kuris et al. (2008) and Hechinger et al. (2011)
Muskingum Brook	USA, New Jersey	Hernandez and Sukhdeo (2008)
Lake Takvatn	Norway	Amundsen et al. (2009, 2013)
Flensburg Fjord	Germany/Denmark	Zander et al. (2011)
Sylt Tidal Basin	Germany/Denmark	Thieltges et al. (2011)

### Increased complexity:

- ↑ Richness
- ↑ Chain length
- ↑ Linkage density

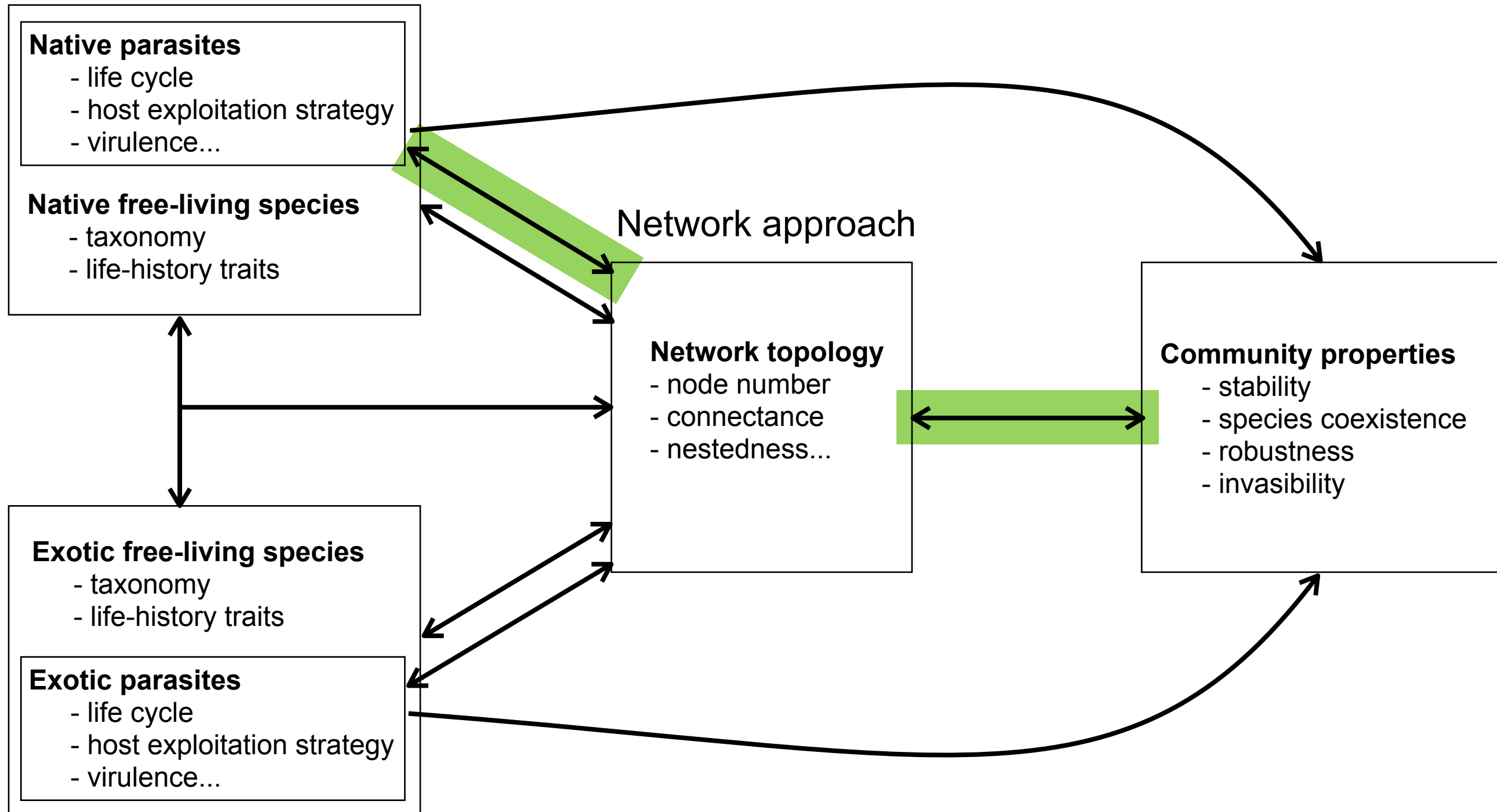
- ↑ Nestedness
- ↑ Connectance

*When parasites are included as taxonomic species*

### Importance of concomitant predation

# Parasites in trophic networks

## Parasite - induced changes in community properties

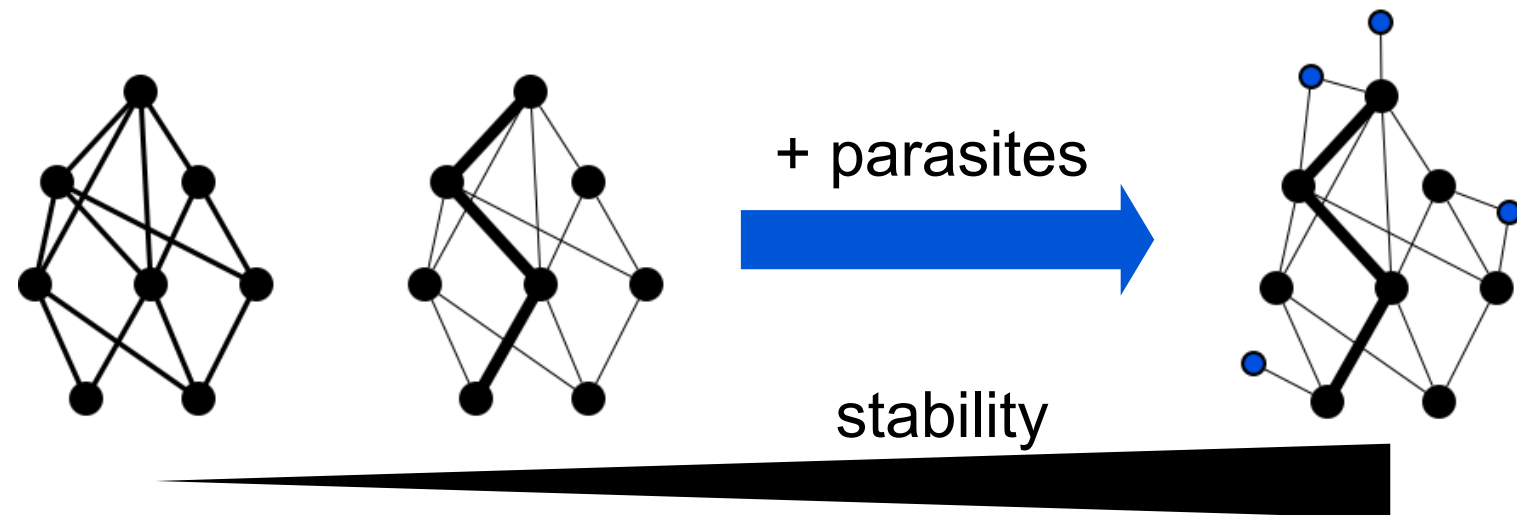


# Parasites in trophic networks

## Parasite - induced changes in community properties

### Parasites and stability

*Following McCann et al. (1998), including parasites should promote stability because they add weak interactions to the network*

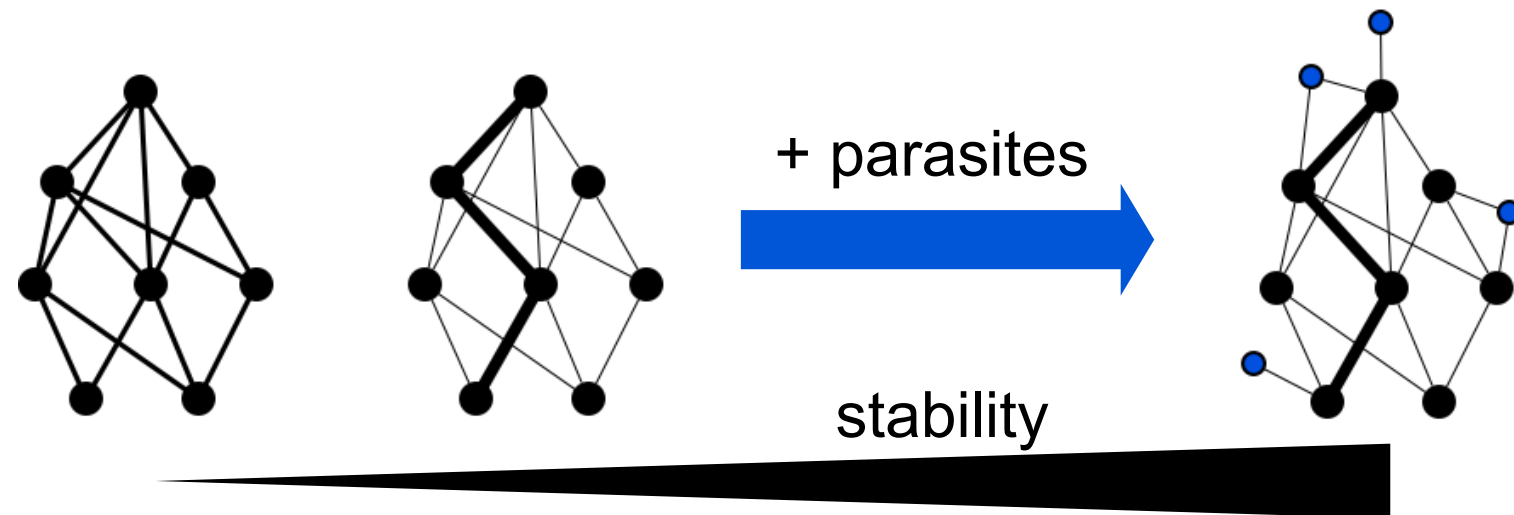


# Parasites in trophic networks

## Parasite - induced changes in community properties

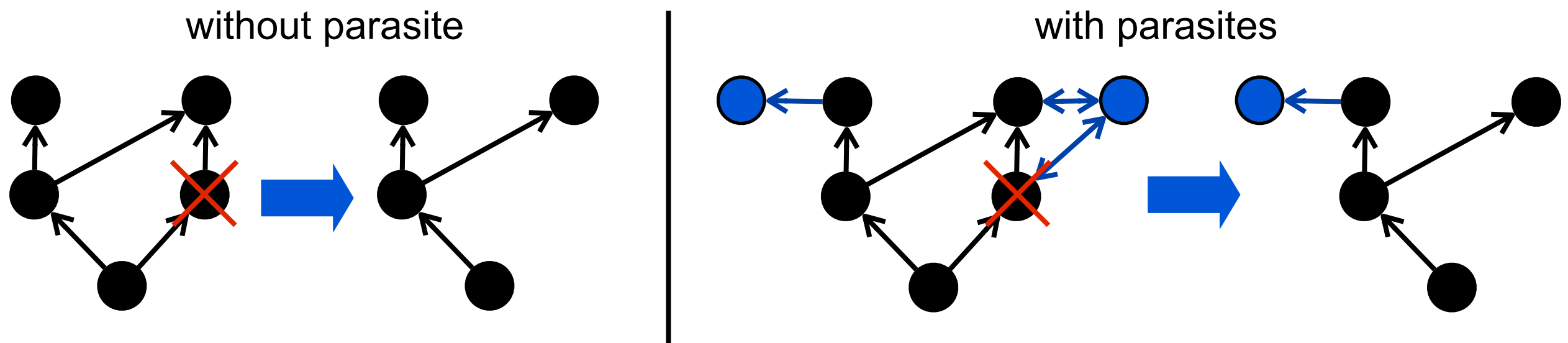
### Parasites and stability

*Following McCann et al. (1998), including parasites should promote stability because they add weak interactions to the network*



### Parasites and robustness

*Parasites should decrease robustness because they increase the risk of secondary extinctions*



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Parasites in invaded networks

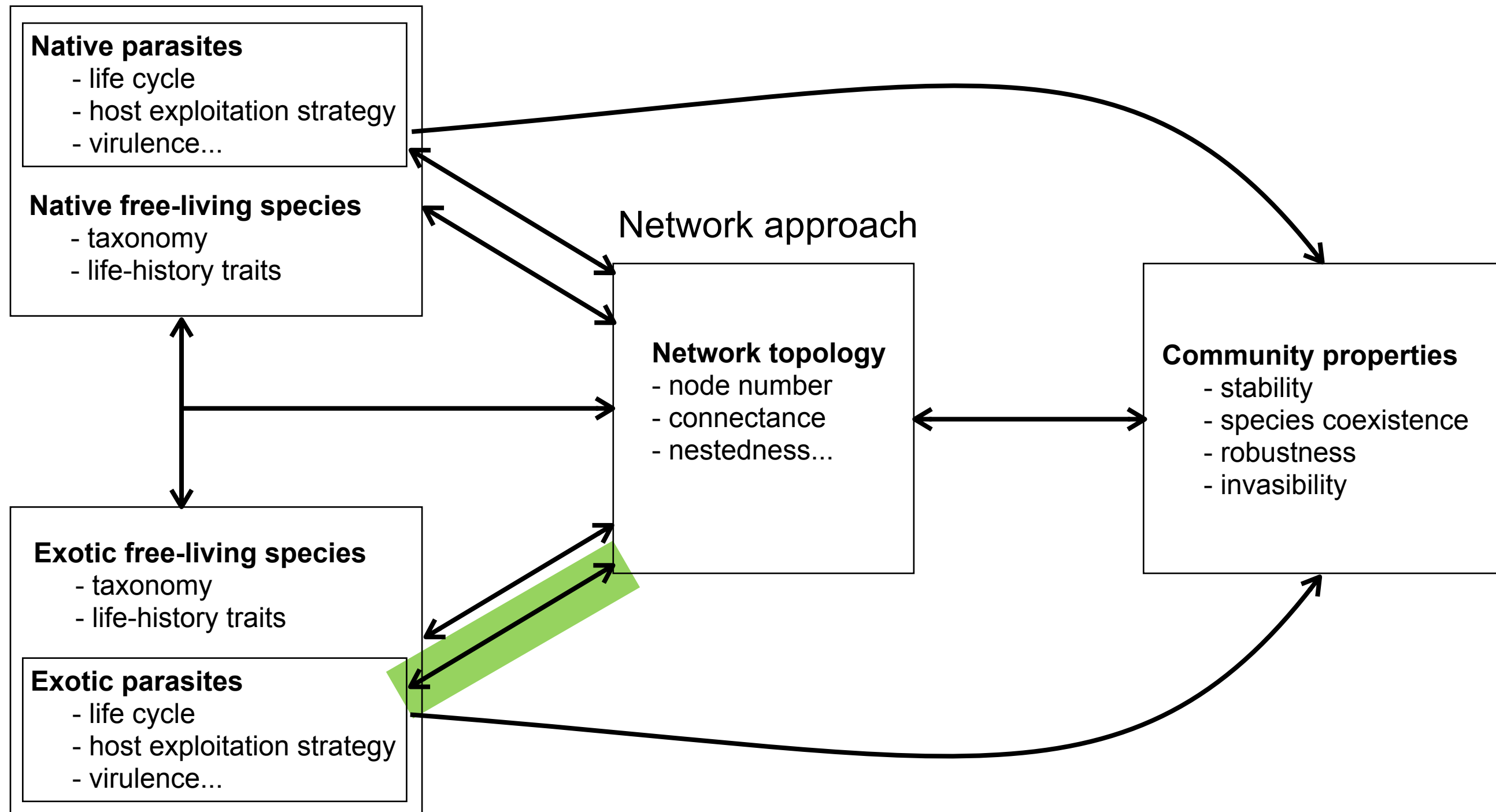
- Impact of introduced parasites on food-web structure

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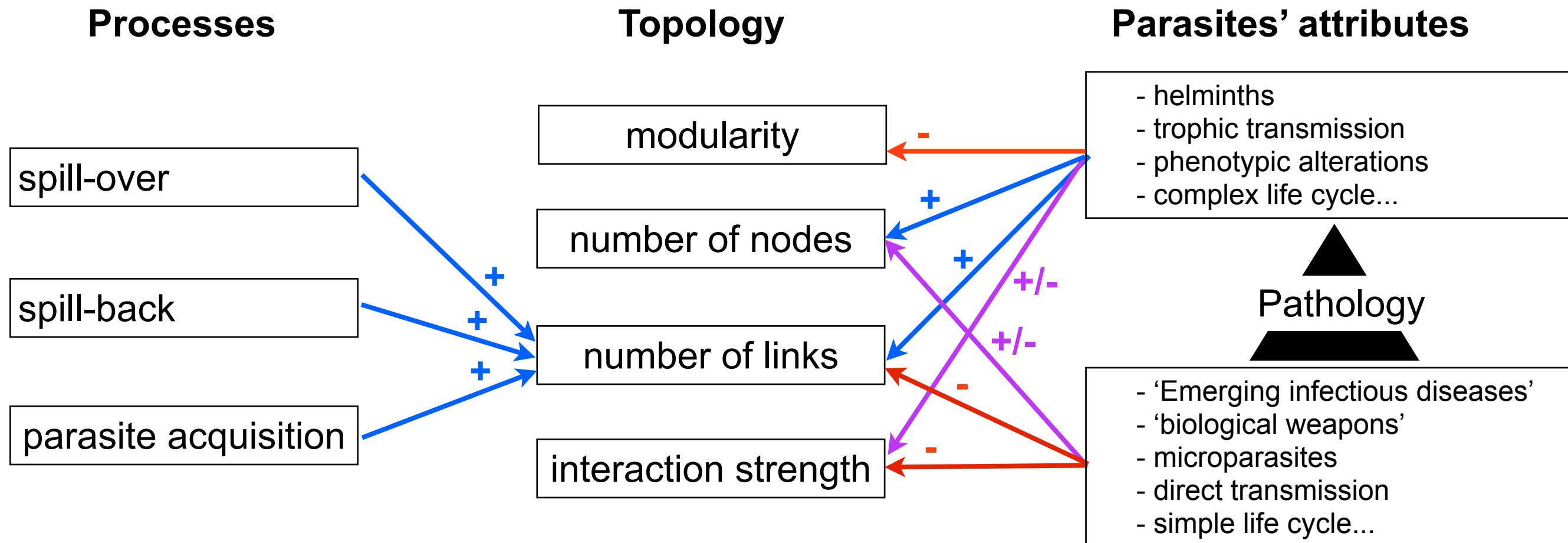
## Impact of introduced parasites on food-web structure





# Parasites in invaded networks

## Impact of introduced parasites on food-web structure



# Parasites in invaded networks

## Impact of introduced parasites on food-web structure

### Processes

spill-over

spill-back

parasite acquisition

### Topology

modularity

number of nodes

number of links

interaction strength

### Parasites' attributes

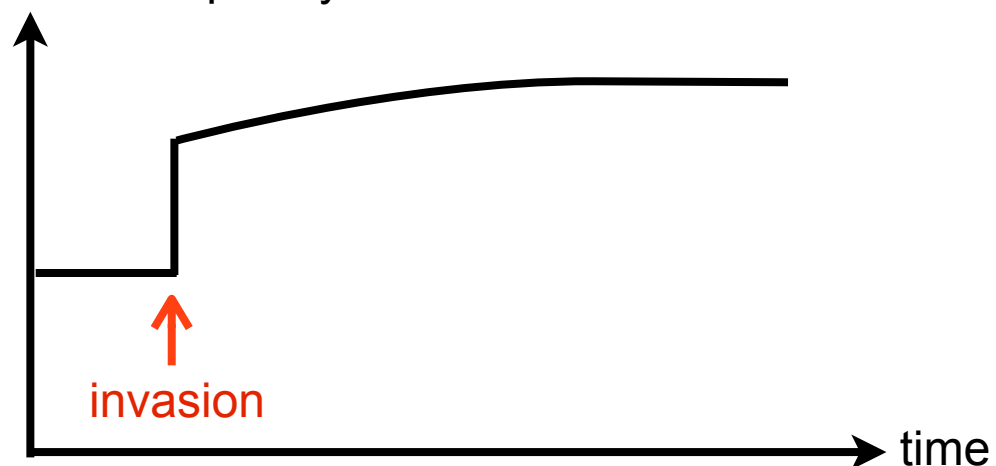
- helminths
- trophic transmission
- phenotypic alterations
- complex life cycle...



- 'Emerging infectious diseases'
- 'biological weapons'
- microparasites
- direct transmission
- simple life cycle...

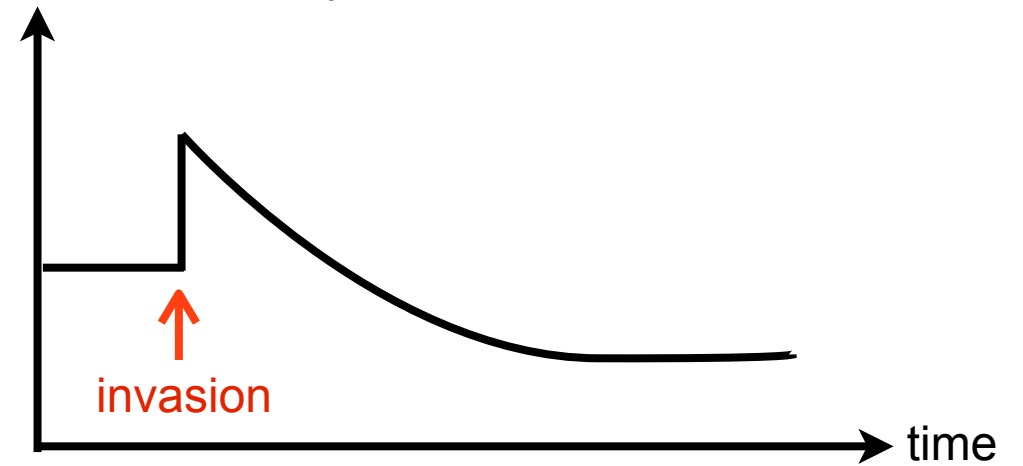
### Parasites with low pathogenicity

network complexity



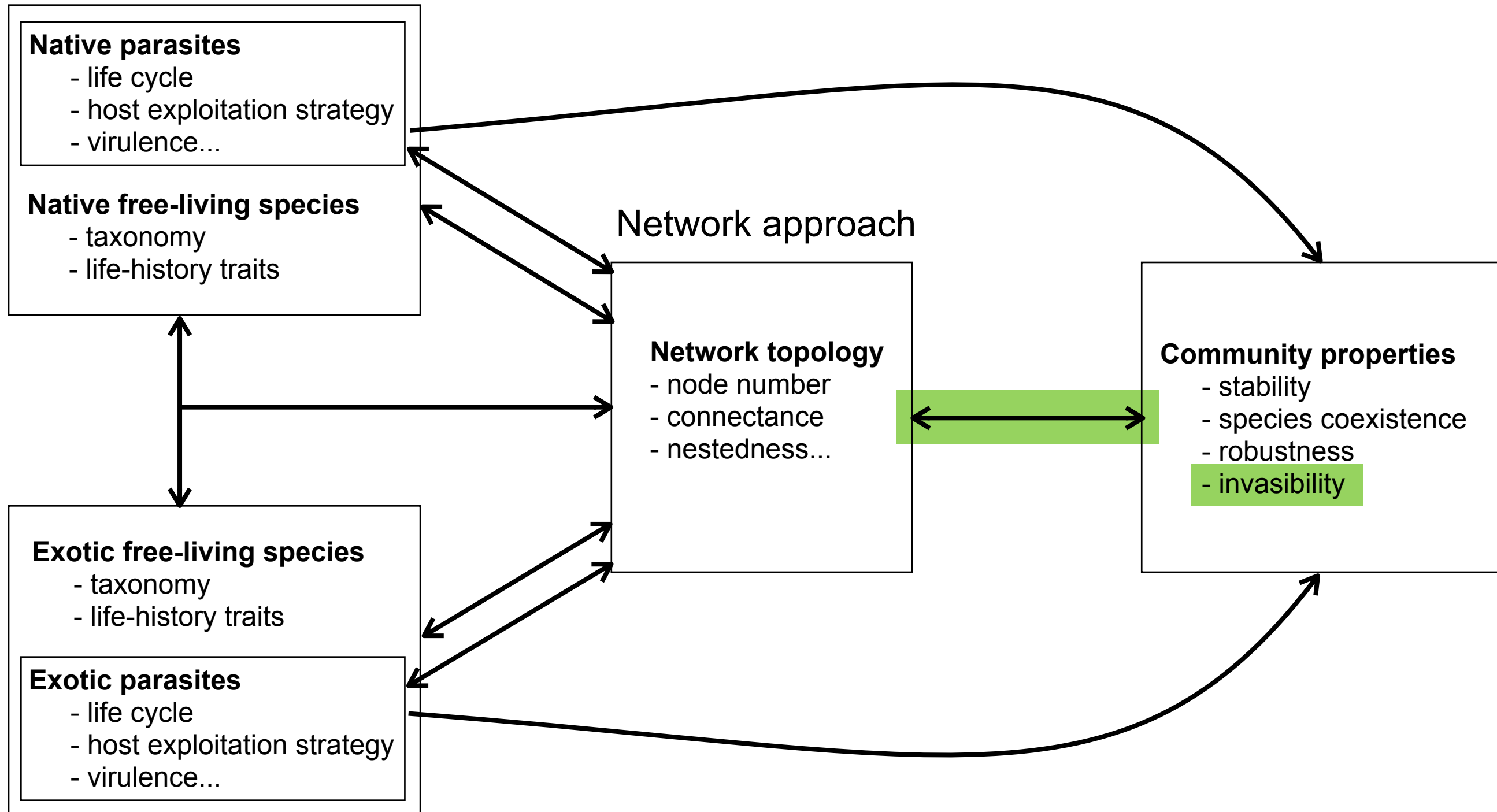
### Parasites with high pathogenicity

network complexity



# Parasites in invaded networks

## Linking network structure and invasibility

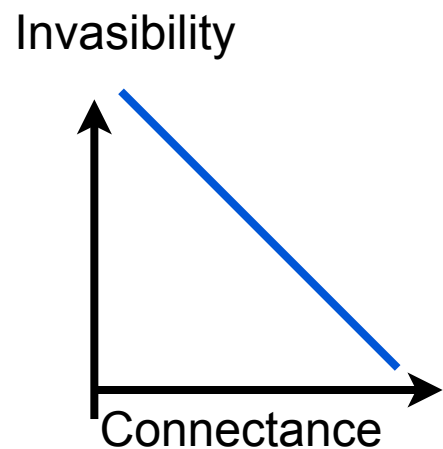


# Parasites in invaded networks

## Linking network structure and invasibility

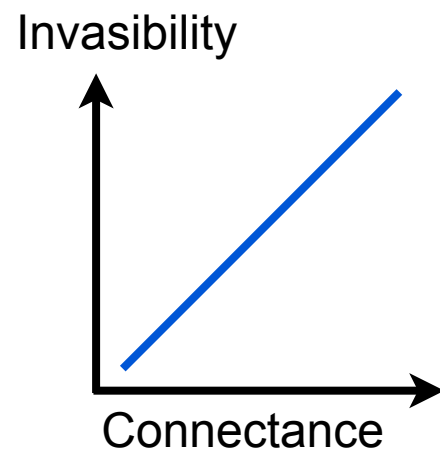
### Connectance and invasibility by free living species

Romanuk et al. (2009) Philos  
Trans R Soc Lond B Biol Sci 364  
Wei et al. (2015) Nat Commun 6

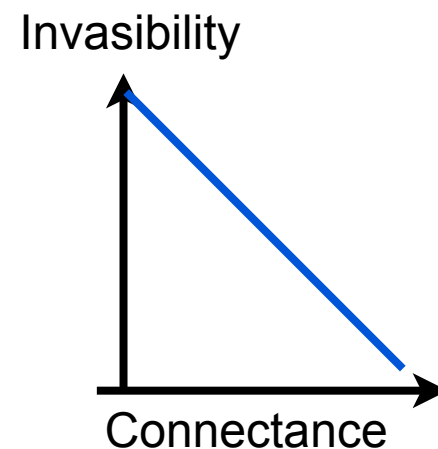


Baiser et al. (2010) Oikos 119  
Vermaat et al. (2009) Ecology 90

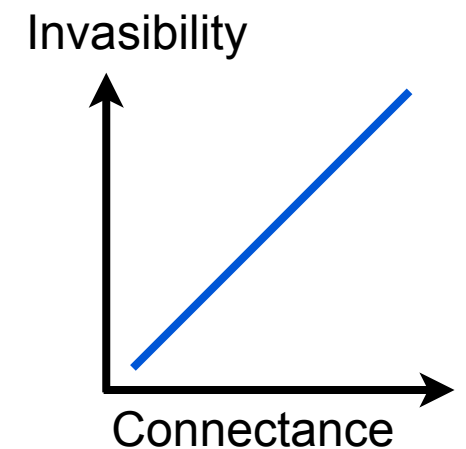
**For exotic top predators**



**For exotic herbivores**



Lurgi et al. (2014) Front Ecol Evol 2  
Hui et al. (2016) Biol Invasions 18



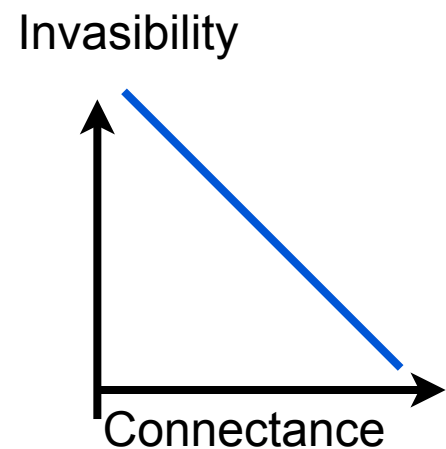
***Opposite predictions...***

# Parasites in invaded networks

## Linking network structure and invasibility

### Connectance and invasibility by free living species

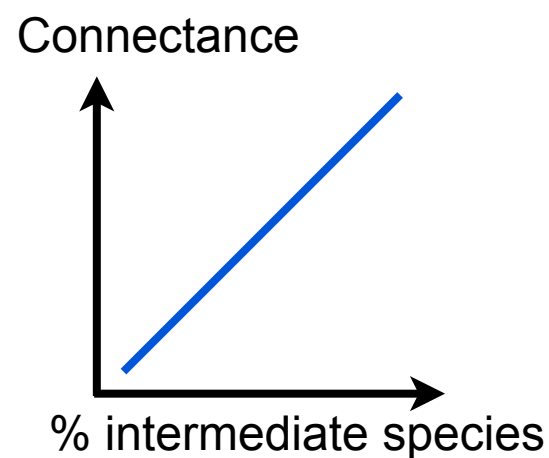
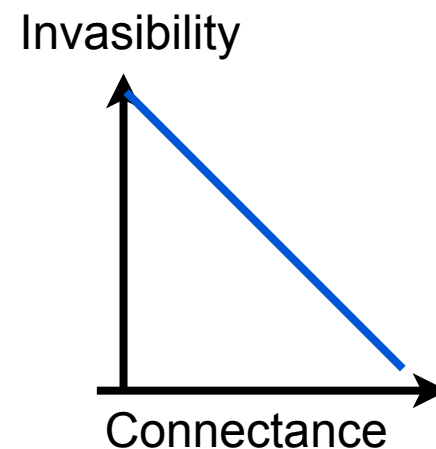
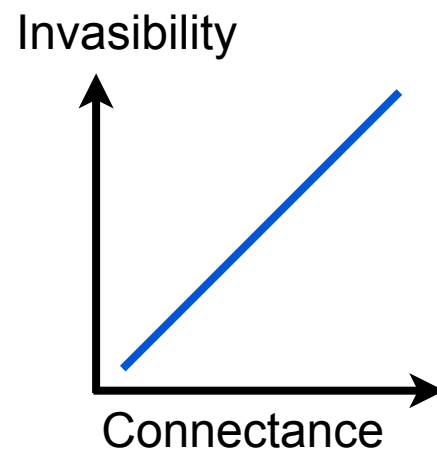
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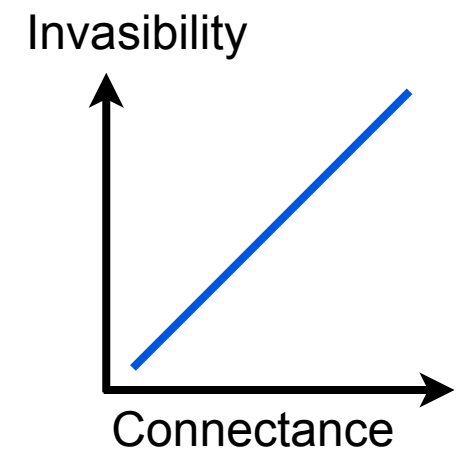
*Increased competition  
and a crowded niche  
space*

Baiser et al. (2010) Oikos 119  
Vermaat et al. (2009) Ecology 90

**For exotic top predators    For exotic herbivores**



Lurgi et al. (2014) Front Ecol Evol 2  
Hui et al. (2016) Biol Invasions 18



*between-species feedbacks:  
they are more important in  
highly connected webs and  
create opportunity niches for  
invasion*

*species diversity:  
- diversity confers  
resistance to invasion  
- more connected webs are  
often less diverse*

# Parasites in invaded networks

## Linking network structure and invasibility

### Connectance and invasibility by co-introduced parasites

Connectance	Species diversity	Invasibility by the co-introduced host	Invasibility by the co-introduced parasite
Low	High	Decreased	Promoted
High	Low	Promoted	Decreased

**Antagonistic effects**

# Parasites in invaded networks

## Linking network structure and invasibility

### Connectance and invasibility by co-introduced parasites

Connectance	Species diversity	Invasibility by the co-introduced host	Invasibility by the co-introduced parasite	Antagonistic effects
Low	High	Decreased	Promoted	
High	Low	Promoted	Decreased	

*Spill-over to native hosts may allow cointroduced parasites to establish in the recipient food web even when its structure constrains invasibility by their cointroduced host.*

*The invasion success of parasites with complex life cycles should decrease with the level of host specificity and the number of successive hosts involved in the cycle.*

# Parasites in invaded networks

## Linking network structure and invasibility

### Modularity and invasibility by parasites

Highly compartmentalized networks are formed by clearly bounded modules, with few interactions between modules, corresponding to spatially or temporally partitioned niches and habitats that are potentially available.

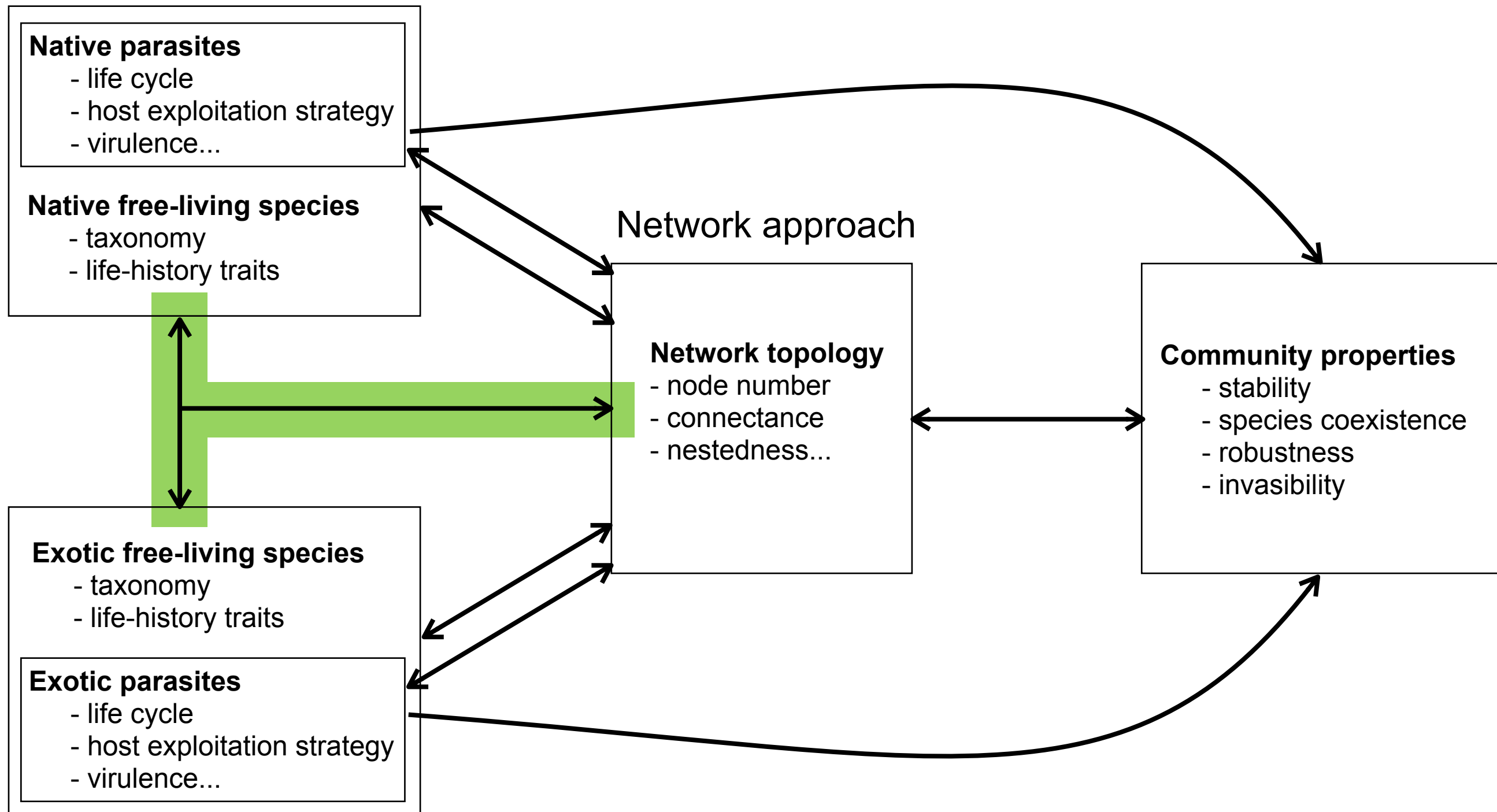


*Complex life cycle parasites experiencing strong ontogenetic niche shifts are more likely to invade highly modular networks, where their probability to meet life cycle requirements in terms of successive hosts and transmission pathways is higher.*



# Parasites in invaded networks

How invader-induced changes in topology affect parasites



# Parasites in invaded networks

## How invader-induced changes in topology affect parasites

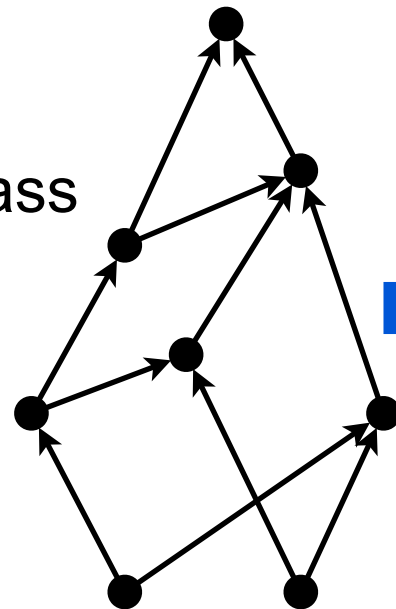
Invasive species:

bio-ecological attributes:

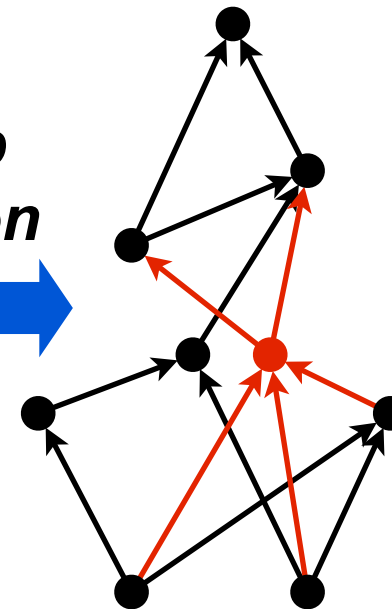
- high abundance and biomass
- broad diet

topological attributes:

- high generality
  - high vulnerability
- 'hubs'***



***food web  
contraction***



- increased connectivity around the invasive species
- reduced connectivity among native species

# Parasites in invaded networks

## How invader-induced changes in topology affect parasites

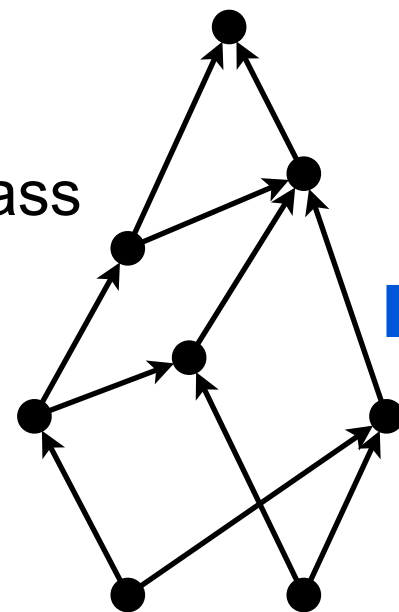
Invasive species:

bio-ecological attributes:

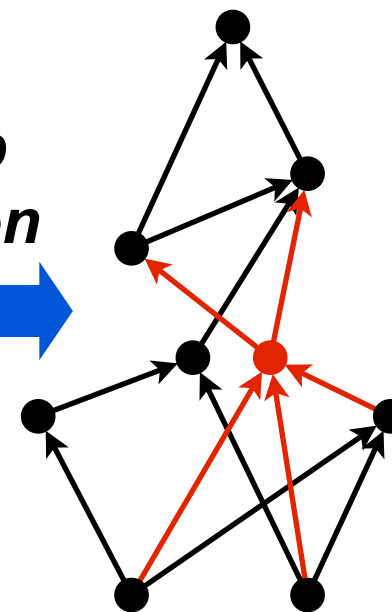
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**food web  
contraction**



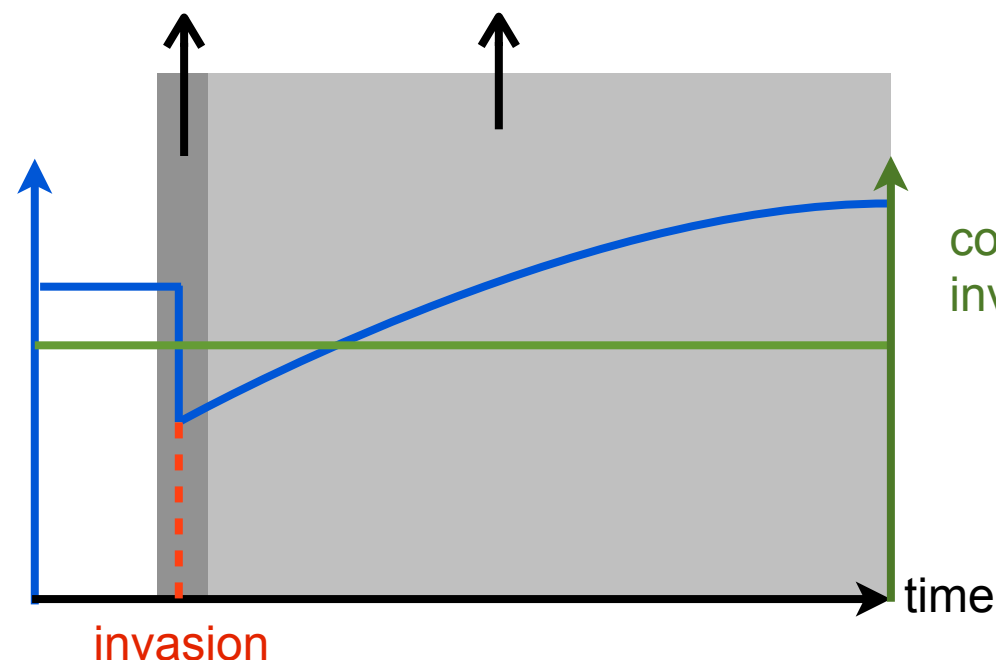
- increased connectivity around the invasive species
- reduced connectivity among native species

**'Enemy Release Hypothesis'**

**'Colonization Time Hypothesis'**

**'Host Centrality' and 'Food Web Contraction'**

nb of parasites in  
the invasive species



connectance of the  
invaded food web

*Invasive species should become important drivers of parasites in recipient ecosystems.*

*Thanks!*