
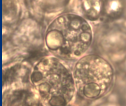




Climate Change and Amphibian Declines

Jason Rohr

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REVIEW

Review and synthesis of the effects of climate change on amphibians

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OUTLINE

- DIRECT LETHAL EFFECTS OF CLIMATE CHANGE AND CLIMATE-INDUCED HABITAT LOSS
- DIRECT EFFECTS OF CLIMATE CHANGE THAT ARE NOT ACUTELY LETHAL
 - (i) changes in phenology
 - (ii) shifts in geographic distributions
 - (iii) body-size reductions
- INDIRECT EFFECTS MEDIATED BY ABIOTIC FACTORS
- INDIRECT EFFECTS MEDIATED BY BIOTIC FACTORS

DIRECT LETHAL EFFECTS OF CLIMATE CHANGE AND CLIMATE-INDUCED HABITAT LOSS

- Several studies suggest that climate change is directly causing amphibian declines by
 - Exceeding upper thermal limits
 - Loss of the Golden Toad (Pounds *et al.* 1999)
 - Reducing water/habitat availability
 - Savannah River Ecology Site (Daszak *et al.* 2005)
 - Yellowstone National Park increase in permanently dry ponds (McMenamin *et al.* 2008)
- Because of the concerns with many of these studies, we still lack convincing evidence that climate change alone has caused declines of amphibians!

DIRECT EFFECTS OF CLIMATE CHANGE THAT ARE NOT ACUTELY LETHAL

- Given that there is little evidence that climate change has been directly lethal to amphibians, if climate change is causing amphibian declines, it is likely doing so through non-acutely lethal or indirect effects (mediated by other organisms or factors) that eventually lead to their demise.
- There are 3 suggested universal responses of species to global warming:
 - (i) changes in phenology
 - (ii) shifts in geographic distributions
 - (iii) body-size reductions (Daufresne *et al.* 2009).

Breeding Phenology

LETTERS

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nature
climate change

Corrected: Publisher correction

Amphibians are shifting their breeding earlier to track climate change.

Although this could have adverse consequences on amphibian fitness or population dynamics, these consequences have not been well studied.

of phenological shifts, suggesting emerging asynchronies between interacting species that differ in body size, such as birds and parasites and predators and prey. Finally, although there are many compelling biological explanations for spring phenological delays, some examples of delays are associated with short-term records that are prone to sampling error. Our findings are consistent with predictions concerning which climatic variables and organismal traits drive phenological shifts.

phenology or body size may be an important factor in determining the magnitude of phenological responses to climate change because smaller organisms acquire more quickly to changing conditions than larger organisms (J.K. Murrell *et al.* 2008). In addition, smaller organisms may exhibit stronger phenological responses than larger organisms because they have more independent of their environments and are therefore more sensitive to changes in environmental conditions. Because of these knowledge gaps, a general global framework is still missing for predicting the direction

Range Shifts

- If amphibians cannot rapidly shift their ranges poleward and up in elevation to track changing climate, there will be lots of amphibian turnover in the future (Lawler et al. 2010)
- If they can, there will be lots of shifts in distributions (Araujo et al. 2006)
- We have some but very limited evidence that amphibians are shifting their ranges poleward or up in elevation, and a limited understanding of the dispersal limitations of amphibians

Shrinking Body Sizes

- Evidence for negative correlations between body size and global warming is available for insects, crustaceans, fish, reptiles, birds and mammals (Gardner et al. 2011; Sheridan & Bickford 2011).
- Caruso et al. (2014) provided evidence consistent with this hypothesis in salamanders, but general evidence in amphibians is scant and much of the evidence is inconsistent.

INDIRECT EFFECTS MEDIATED BY ABIOTIC FACTORS

- Hof et al. (2011) assess the spatial distribution and interaction of 3 threats to amphibians:
 - climate change,
 - land-use change
 - chytrid fungus
- Regions with the highest projected change in land-use and climate coincide, but largely do not overlap with the highest areas of chytrid suitability.
- Future habitat loss and climate change are more likely to additively or synergistically interact to affect amphibians than are future habitat loss and chytrid or climate change and chytrid.

INDIRECT EFFECTS MEDIATED BY ABIOTIC FACTORS

- Several studies suggest that climate change could increase exposure to or toxicity of chemical contaminants (Noyes *et al.* 2009, Kattwinkel *et al.* 2011, Rohr *et al.* 2013, but see Rohr *et al.* 2011), which might facilitate declines

INDIRECT EFFECTS MEDIATED BY BIOTIC FACTORS

- Primary focus of talk will be on climate-disease interactions


Chytridiomycosis

- Caused by the fungus *Batrachochytrium dendrobatidis* (hereafter referred to as Bd)
- Skin disease that likely causes cardiac arrest
- Implicated in hundreds of amphibian extinctions in the last four decades
- Possibly the most deadly invasive species on the planet behind humans

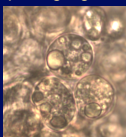


Amphibian chytrid fungus (*Bd*)

Direct Developing

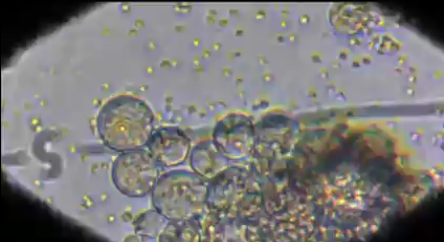


Zoospores grow on skin



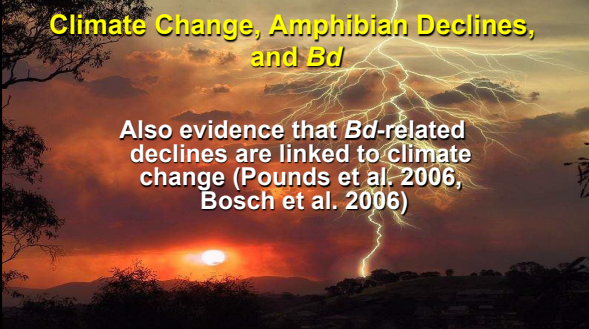
Believed to grow best at cool-moderate temperatures (18-21 °C)

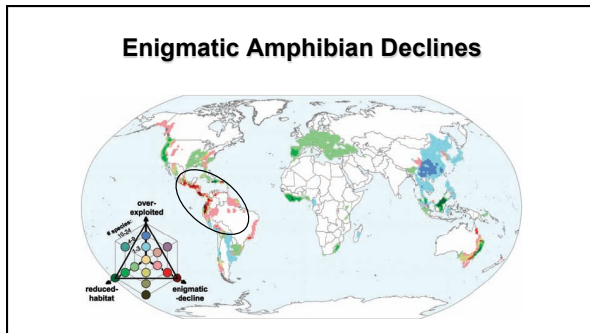
Chytrid fungus that causes amphibian chytridiomycosis



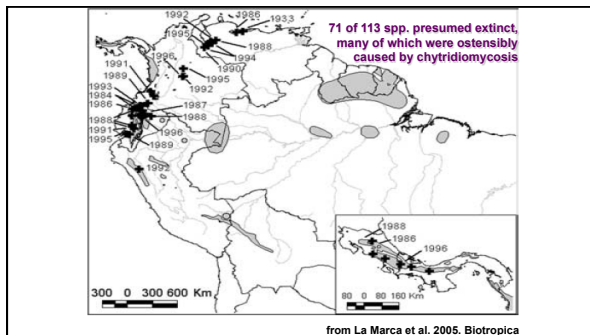
Climate Change, Amphibian Declines, and *Bd*

Also evidence that *Bd*-related declines are linked to climate change (Pounds et al. 2006, Bosch et al. 2006)

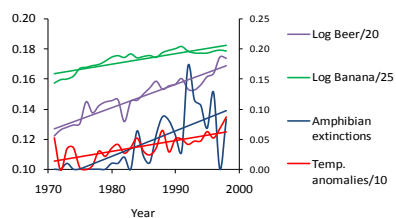








Tenuous Links Between Climate and Amphibian Declines



Rohr et al. 2008 PNAS

Need to Conduct Detrended Analyses?

- If there is a true relationship between climate and *Bd*-related extinctions, fluctuations around temporal trends in temperature and extinctions should also positively correlate
- There would many fewer non-causal explanations for this correlation than the multidecadal relationship between declines and temperature

Objectives

Use the *Ateopus* database to simultaneously test various climate-related hypotheses for amphibian declines, controlling for multidecadal correlations and the intrinsic spatiotemporal spread of *Bd*

Proximal Hypotheses for Enigmatic/*Bd*-related Declines

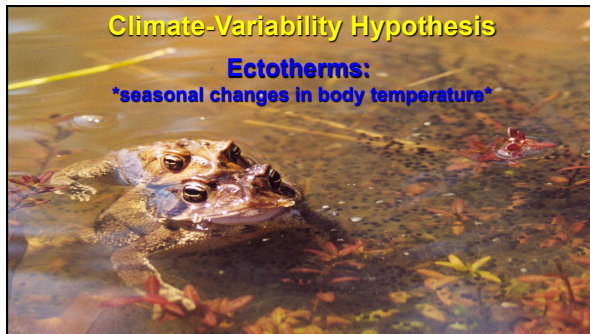
Spatiotemporal-spread hypothesis: declines are caused by the introduction and spread of *Bd*, independent of climate (Bell et al. 2004, Lips et al. 2006)

Climate-based hypotheses:

Chytrid-thermal-optimum hypothesis: Increased cloud cover, due to warmer oceanic temperatures, leads to temperature convergence on the optimum temperature for growth of *Bd* (Pounds et al. 2006, Bosch et al. 2006)

Mean-climate hypothesis: changes in mean temp. and/or moisture conditions affect the distributions of amphibians (Whitfield et al. 2007, Buckley & Jetz 2007)

Climate-variability hypothesis: temporal variability in temp. cause suboptimal host immunity facilitating declines (Raffel, Rohr, et al. 2006)



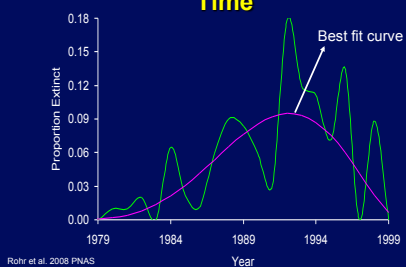
Climate Variability Hypothesis

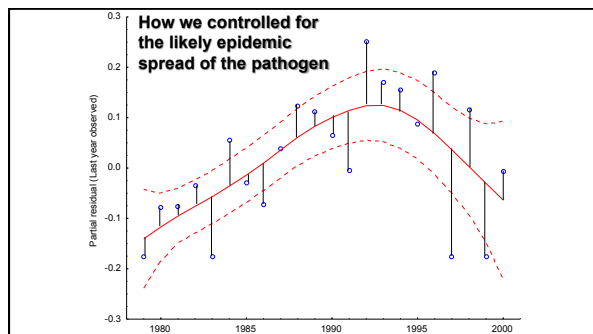
- Hypothesis: unpredictable temperature shifts, which are increasing with GCC, benefit pathogens more than hosts.
 - acclimate more quickly to unpredictable temperature shifts, especially for ectothermic hosts
 - fewer cells and processes to adjust (Portner 2002)
 - evolve more quickly to changes in climate

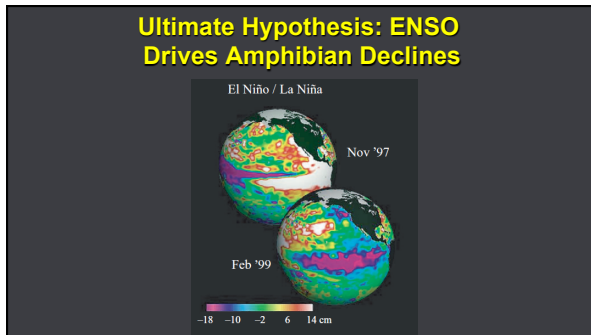
Climate Variability Hypothesis

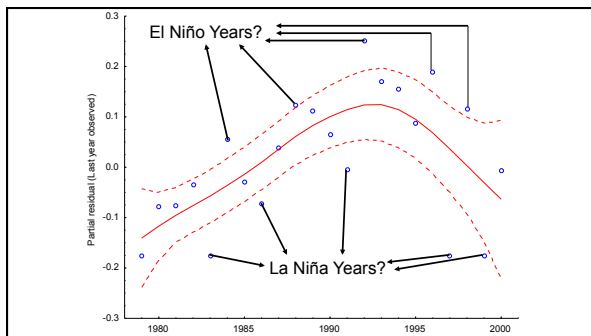
- The categorically faster metabolisms, smaller size, and greater reproductive capabilities of parasites than hosts provides a general hypothesis for how global climate change will affect disease risk– **unpredictable climate variability should increase disease.**

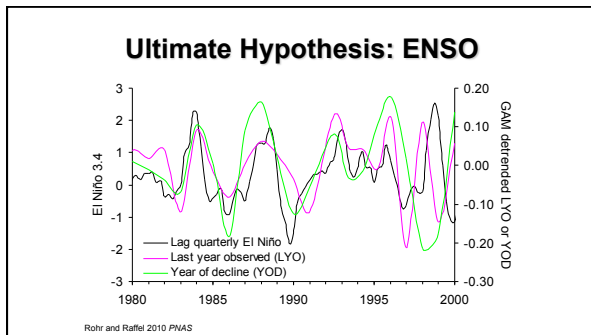
Atelopus Extinctions Through Time











Must Control for Intrinsic Dynamics to Detect Extrinsic Factors!

- No significant ENSO signature if we don't control for probable epidemic spread
- Hence, the availability of susceptible hosts appears the primary factor influencing epidemic spread followed secondarily by climate

But What is the Proximate Explanation?

What is it about El Nino years that is associated with amphibian extinctions?

Proximal Hypotheses for Enigmatic/*Bd*-related Declines

- **Spatiotemporal spread hypothesis:** declines are caused by the introduction and spread of *Bd*, independent of climate (Bell et al. 2004, Lips et al. 2006)
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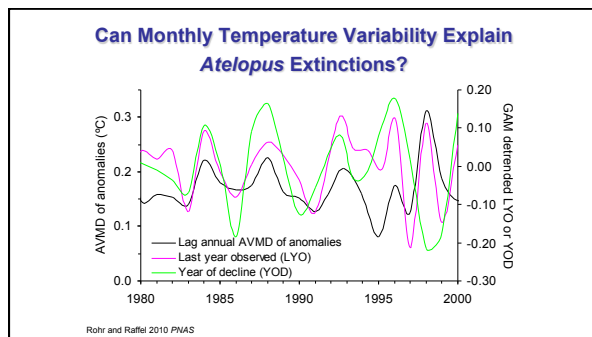
Regional Predictors tested w/ and w/o a one year lag

1. Mean absolute value of monthly differences (AVMD) in temp.
2. Cloud cover x temp. (Pounds et al. 2006)
3. Cloud cover (Pounds et al. 2006)
4. Temperature-dependent *Bd* growth (Pounds et al. 2006)
5. Precip. x temp. (Whitfield et al. 2007)
6. Diurnal temp. range
7. Frost freq.
8. Precip.
9. Temp.
10. Temp. max.
11. Temp. min.
12. Vapor press.
13. Wet day freq.

Results of Best Subset Model Selection

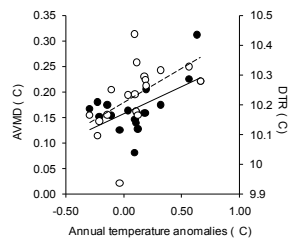
Model Ranking	Adjusted R ²	No. of effects	t			t-1					
			Precip.	Wet day freq.	AVMD temp.	Cloud cover	Diurnal temp. range	Temp. max.	Temp. min.	Vapor Pres.	
1	0.685	3	0.253		0.859		0.764				
2	0.671	3		0.230	0.845		0.755				
3	0.644	3			0.857	0.15	0.692				
4	0.643	3			0.804		0.788				0.212
5	0.640	3			0.807		0.738			0.177	
6	0.640	3			0.807		0.693	0.161			
7	0.640	3			0.807		0.849		0.157		
8	0.640	3			0.806			-2.350	2.453		
9	0.640	2			0.892		0.699				
10	0.640	3			0.892				1.306	-1.286	

results are similar using AIC



Amphibian extinctions have often occurred in warmer years, at higher elevations, and during cooler seasons.

Do Warmer Years Have Greater Variability in Temperature?



Rohr and Raffel 2010 PNAS

Do High Elevations Have Greater Variability in Temp.?

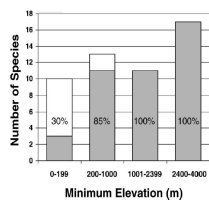
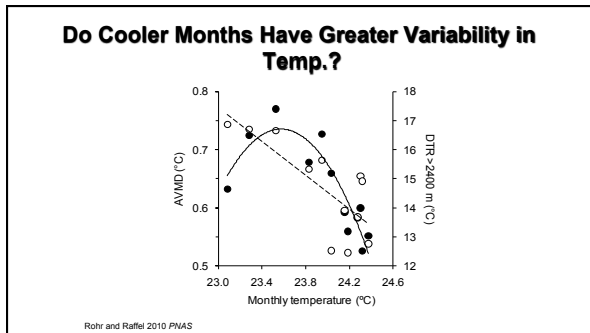
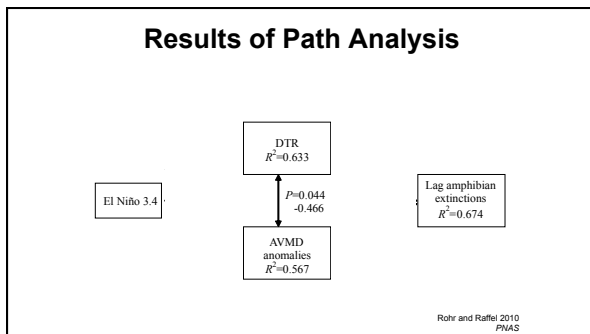
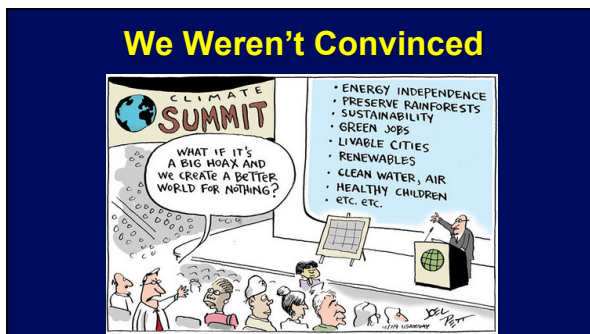


Figure 7. Percentage of Anolis Species Declined or Extinct by Elevation in our Study Area.
 Bars show the number of species at each elevation category while gray depicts the number of species in decline and white depicts stable species. The percentage of species in decline is written on each bar. Total number of species included in the analysis was 51.





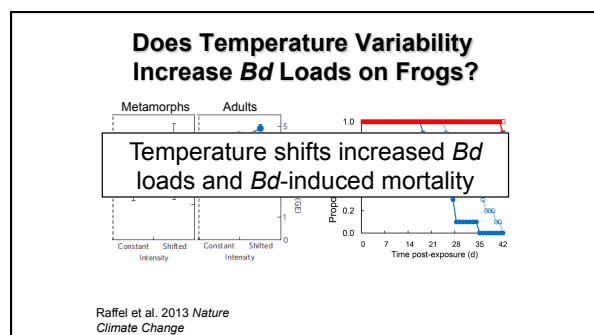


Experimental Test

- Acclimated Cuban tree frogs to 15 or 25° C for four weeks
- Challenged with *Bd*, *Aeromonas hydrophila*, or *Rhabdias* sp. at start of week five
- Quantified survival and pathogen loads







Summary

- Availability of susceptible hosts appears to be the primary factor influencing the spread of *Bd*
- There is a strong ENSO signature to extinctions after controlling for epidemic spread
- Both field patterns of extinctions and manipulative experiments support the climate-variability hypothesis for amphibian extinctions

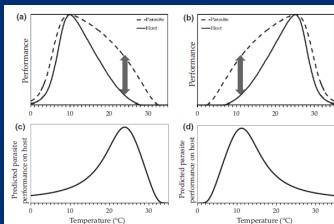
REFINING OUR IDEAS

Infectious Diseases and Climate

- Although it is clear that extreme temperature events cause disease outbreaks, neither warm nor cold spells universally increase outbreaks.
- Thus, more nuanced hypotheses regarding the effects of weather and climate on disease are necessary.
- These more nuanced hypotheses need to be tested against the climate variability hypothesis!

Thermal mismatch hypothesis

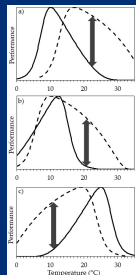
Hosts should be more susceptible to disease at conditions far from those they routinely experience



Hosts and parasites are locally adapted to conditions

Parasites have greater performance breadth than hosts

Thermal mismatch hypothesis



Predictions of the *thermal mismatch hypothesis* are robust to the underlying assumptions:

- 1) locally adaptation
- 2) right- and left skew

128 thermal response curves of ectotherms with body mass, latitude, habitat, acclimation duration and temp.

13 orders of magnitude in body masses

Do Parasites Really Have Broader Thermal Breadths than Hosts?

Systematic variation in the temperature dependence of physiological and ecological traits

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Edited by James Hensleigh Brown, University of New Mexico, Albuquerque, NM, and approved April 28, 2011 (received for review October 14, 2010)

To understand the effects of temperature on biological systems, we compile, organize, and analyze a database of 1,072 thermal responses for microbes, plants, and animals. The unprecedented diversity of traits (n = 110, species n = 260, body sizes [10 orders of magnitude], and habitats [all major biomes]) in our database allows us to quantify novel features of the temperature response of biological traits. In particular, analysis of the rising component of ecto-species (interspecific) response reveals that 87% are fit well by the Boltzmann-Arrhenius model. The mean activation energy for these fits is 0.68 ± 0.05 eV, similar to the reported across-species (interspecific) value of 0.65 eV. However, systematic variation in the distribution of our activation energies is evident, including previously unrecognized right skewness around a median of 0.55 eV. This skewness exists across levels of organization, taxa, trophic groups, and habitats, and it is partially explained by prey heating

describe patterns that suggest mechanisms responsible for generalities and deviations in the thermal dependence of biological traits. We compile data on both physiological and ecological traits but focus on those central to species interactions (Fig. 1, Appendix, Table S1). The thermal response of interaction traits can be strongly influenced by organismal behavior (22–25), so we focus on how biological processes are executed (e.g., attack body velocity, handling rates) and not on decisions (e.g., attack probability, decision to behave) probably above whether to execute them. Requiring each response to have numerous measurements at a minimum of four distinct temperatures that cover a range of at least 3 °C yields 1,072 responses. Our ontology categorizes these responses into 112 distinct traits that span levels of biological organization from internal physiology to species interaction (Fig. 1 and Appendix and Methods). Traits were measured in marine, freshwater, and terrestrial habitats for 309 species of plants,

What is the relationship between body

Both the model and data, support breadth increasing with latitude and decreasing with body size. Consistent with reviews on this topic (Baas-Becking 1934; Martiny et al. 2006).

The figure consists of two parts: 'Theoretical predictions' and 'Empirical data'. Both parts show a graph of relative fitness (y-axis) versus temperature (x-axis). In the theoretical predictions, a single curve shows a broad peak, indicating a large thermal breadth. In the empirical data, multiple curves are shown, each with a narrower peak, indicating a smaller thermal breadth. Below these graphs, a line graph shows 'relative fitness' on the y-axis and 'temperature' on the x-axis. It features a bell-shaped curve representing the thermal performance of an organism. The 'performance breadth' is the width of the curve at a given fitness level, and the 'tolerance range' is the total width of the curve. The curve is labeled with CT_{min} and CT_{max} at its base.

Diversity in growth patterns among strains of the lethal fungal pathogen *Batrachochytrium dendrobatidis* across extended thermal optima

***Bd* has a larger thermal breadth than its hosts**

constrain pathogen reproductive rates. Amphibian chytridiomycosis, caused by the pathogen *Batrachochytrium dendrobatidis* (*Bd*), is a lethal fungal disease that is influenced by temperature. However, recent temperature studies have produced contradictory findings, suggesting that our current understanding of thermal effects on *Bd* may be incomplete. We investigated how temperature affects three different *Bd* strains to evaluate diversity in thermal responses.

higher logistic growth rates (*r*) and carrying capacities (*K*) at the upper and lower extremities of the temperature range, and especially in low temperature conditions (2–3 °C). In contrast, a third strain exhibited relatively lower growth rates and carrying capacities at these same thermal extremes. Overall, our results suggest that there is considerable variation among *Bd* strains in thermal tolerance, and they establish a new thermal sensitivity profile for *Bd*. More generally, our findings point toward important questions concerning the mechanisms that dictate fungal thermal tolerances and temperature-dependent pathogenesis in other fungal disease systems.

Outline

- 1) Test the *thermal mismatch hypothesis* experimentally across three host species by quantifying
 - (a) temperature-dependent host performance in isolation
 - (b) temperature-dependent parasite performance in isolation
 - (c) temperature-dependent performance of host and parasite when interacting
- 2) Assess the generality of the *thermal mismatch hypothesis* using amphibian field prevalence and sample-specific climate data
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Temperature-Dependent Experiments



A. terrestris

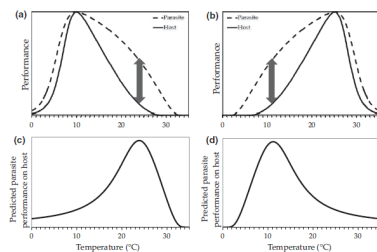


O. septentrionalis

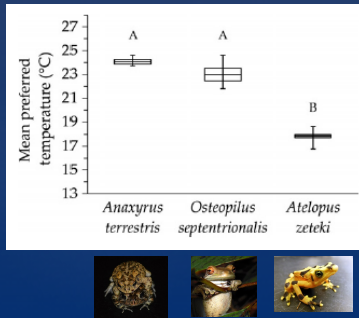


A. zetekii

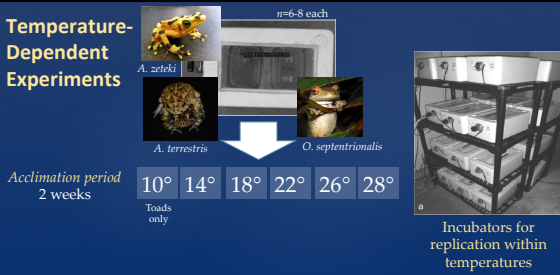
Hypothesis



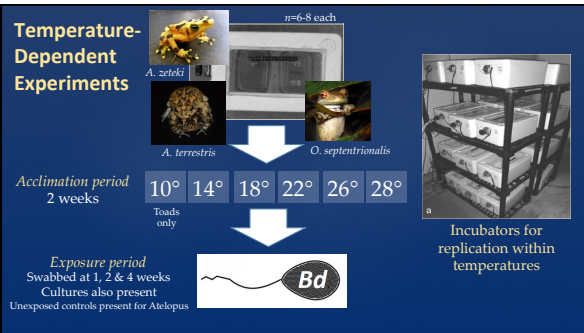
Temperature-Dependent Experiments: Thermal preference trials

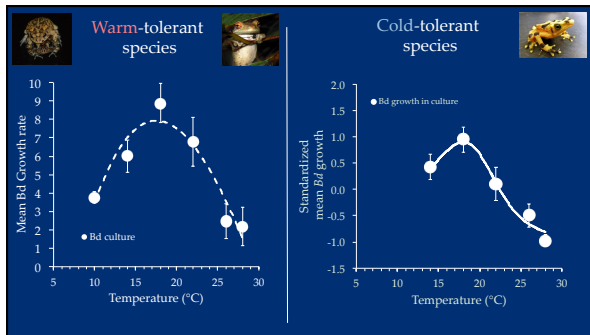


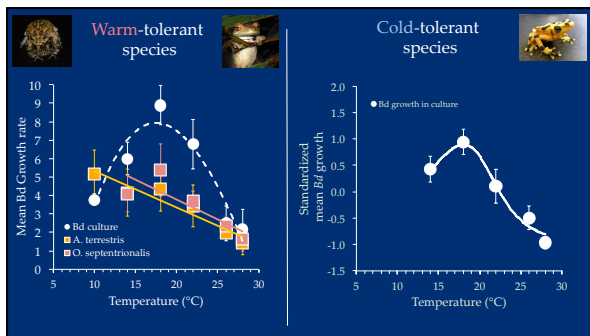
Temperature-Dependent Experiments

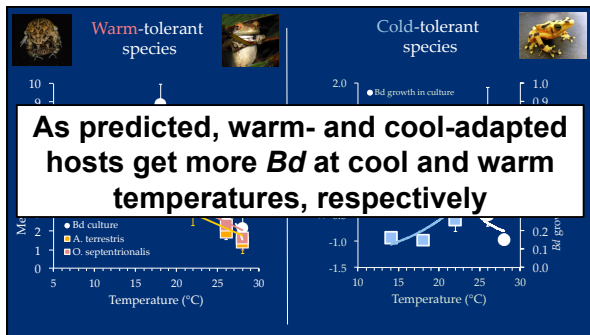


Temperature-Dependent Experiments









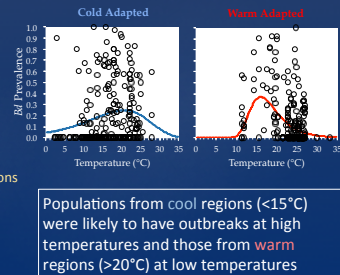
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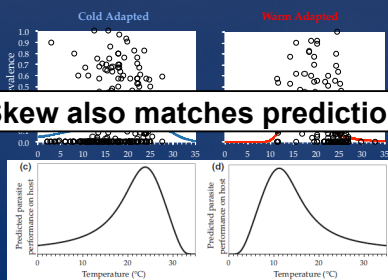
Bd outbreaks and temperature across populations

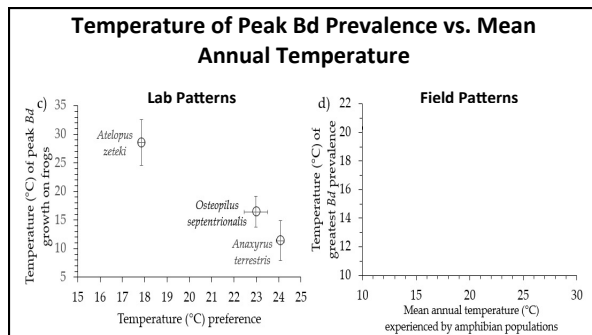
Collected Bd prevalence data for 15,410 individuals in 598 populations from 250 published papers

Collected climate data from the months and locations those populations were tested

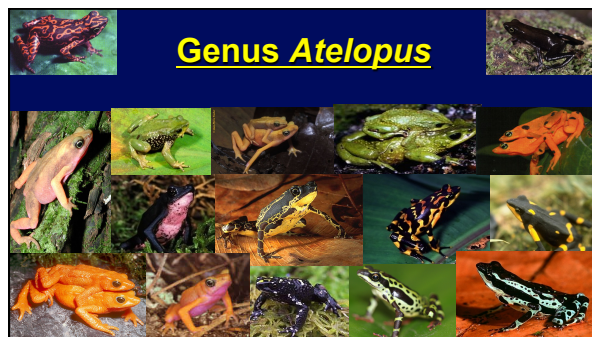


Skew also matches predictions



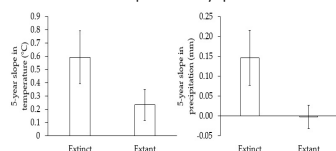


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Need to verify that climate change was associated with extinctions based on data from individual species' ranges

- In the geographic ranges of species that went extinct, mean temperatures in the five years leading up to extinction increased ~2.5 times faster than they increased in the ranges of species that remained extant ($F_{1,45}=7.73$, $p<0.01$).
- Soon-to-be extinct species were experiencing conditions that were unusually warm for them and warmer than those experienced by species that remained extant.



Set out to parameterize our statistical model by conducting laboratory experiments to evaluate the impacts of both mean temperature and temperature variability on *Atelopus* spp. mortality risk

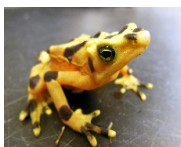
A Hypothetico-Deductive Approach: Six Predictors for Extinctions

- a null model
- pathogen alone**: temperature-dependent growth of *Bd* in culture
- temperature variability alone**: annual month-to-month variability in temperature
- mean climate alone**: annual mean temperature
- climate change alone**: the 5-year slope of mean temperature
- the interaction between mean historical climate and climate change: because the **thermal mismatch hypothesis** predicts that the effect of climate change depends on whether the host is cool or warm adapted, which in turn drives the differential performance of host and pathogen.

Temperature Variability Study Methods

- A. zeteki* were exposed to *Bd* at 14°, 17°, 20°, 23°, or 26°C immediately following either two weeks of acclimation to these temperatures for constant group or two weeks of acclimation to 20°C for shifted group

Constant	Shifted (acclimated at 20°)
14°	14° (-6°)
17°	17° (-3°)
20°	20° (-0°)
23°	23° (+3°)
26°	26° (+6°)

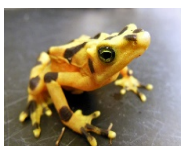


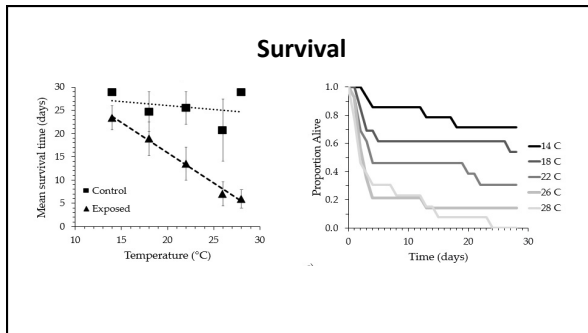
Temperature Variability Study Results

- Bd*-induced mortality increased with temperature ($p < 0.05$).
- At the same *Bd* exposure temperatures, frogs that experienced temperature shifts had higher *Bd* loads than those that did not experience shifts ($p = 0.005$).
- We did not observe any significant effect of the temperature shift treatment on mortality ($p = 0.36$).
- The temperature gradient accounted for >6 times the variance in *Bd*-induced mortality as temperature variability.

Mean Temperature Methods

- A. zeteki* were maintained at 14°, 18°, 22°, 26°, or 28°C and exposed to *Bd* or not.





Specific Hypotheses for Extinction Analyses

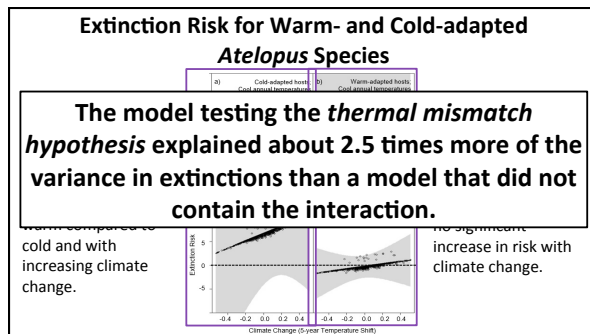
- *Bd* growth in culture, temperature variability, and mean temperature alone would be poor predictors of *Atelopus* extinctions relative to the *thermal mismatch hypothesis*
- The *thermal mismatch hypothesis* would be the best predictor
 - would manifest as a statistical interaction between the temperature to which a species is adapted and the level of climate change it has experienced

Time-dependent cox-proportional hazards survival model accounting for spatiotemporal spread

- Model evaluated the following predictors of the occurrence and timing of extinctions:

-- <i>thermal mismatch hypothesis</i>	-- <i>Bd</i> growth in culture
-- temperature variability	-- precipitation
-- mean temperature	-- altitude
-- climate change	-- geographic range size
- Used information criteria to select among multiple gravity models to account for spatiotemporal spread of *Bd*
 - distance from nearby extinctions
 - size of nearby extinctions

Survival Model				
Effect	Coefficient	Robust SE	z	p
Neither precipitation, altitude, spatial spread, mean temperature, <i>Bd</i> growth in culture, or temperature variability explained significant variation in <i>Atelopus</i> spp. extinction risk				
Culturemortprob (pathogen only)	-1.16E+00	1.23E+00	-0.95	0.344
Range size	-2.22E+01	5.21E+01	-0.43	0.669
Log(AVMD) (temp. variability)	9.07E-01	7.13E-01	1.27	0.204
Tempchange (climate change only)	1.17E+01	3.73E+01	0.31	0.754
dbyr meantemp (cold or warm adapted)	1.28E+00	7.66E-01	1.67	0.095
Meantemp (mean temp. only)	5.89E-01	7.60E-01	0.78	0.438
Latitude	-1.37E-01	1.49E-01	-0.92	0.355
Total precipitation	1.39E+05	1.59E+05	0.88	0.380
Frequency of wet days	-1.77E-05	5.04E-05	-0.35	0.726
Distance from nearby extinctions	-4.41E-02	8.74E-02	-0.50	0.614
Range size: Culturemortprob	-9.82E+00	6.74E+00	-0.57	0.572
Range size: log(AVMD)	-1.50E+00	1.86E+00	-0.81	0.420
Range size: Tempchange	-1.66E+02	8.48E+01	-1.96	0.050
Range size: dbyr meantemp	1.43E+00	2.92E+00	0.49	0.625
Tempchange: dbyr meantemp	1.54E+03	2.79E+00	0.00	1.000
Range size: meantemp	3.00E+00	4.08E+00	0.74	0.461
Tempchange: meantemp	3.47E-01	2.17E+00	0.16	0.873
dbyr meantemp: meantemp	-5.14E-02	3.26E-02	-1.58	0.115
Range size: Tempchange: dbyr meantemp	1.17E+01	5.04E+00	2.32	0.021
Range size: Tempchange: meantemp	6.13E+00	6.33E+00	0.97	0.333
Tempchange: dbyr meantemp: meantemp	-1.41E-01	1.96E-01	-0.72	0.473
Tempchange: dbyr meantemp: meantemp	-2.81E-02	1.10E-01	-0.25	0.799
Range size: Tempchange: dbyr meantemp: meantemp	-4.79E-01	2.23E-01	-2.15	0.032



Conclusions

Host species are more susceptible to disease at temperatures far from those to which they are adapted

Cold-adapted species may be vulnerable to disease at warm temperatures, and vice-versa

Climate change may put cold-adapted hosts at greater risk of disease, but increasing extreme weather could put all hosts at greater risk

Our findings help explain the tremendous variation in species responses to *Bd* across climates and spatial, temporal, and species-level variation in disease outbreaks associated with extreme weather events that are becoming more common with climate change.

Conclusions (cont.)

- By combining experiments with field patterns to examine how mean temperature and temperature variability impact *Atelopus* susceptibility to *Bd*, we provide
 - support for the *thermal mismatch hypothesis*, and
 - the first evidence that one of the greatest modern day mass extinctions was likely driven by an interaction between climate change and infectious disease.

Acknowledgements

Main Collaborators

Jeremy Cohen
Dave Civitello
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Katherine Vasquez
Kim Ebener



WorldClim

Can Climate Change Alone Explain these Results?

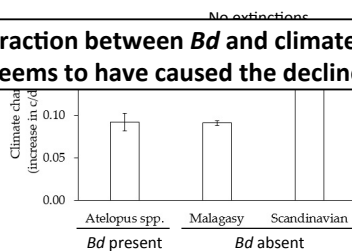
- It seems unlikely that *Bd* alone was the cause of *Atelopus* spp. extinctions because if it was, one would not expect to observe a climate change signal.
- We set out to gather more support against the hypothesis that climate change alone drove these extinctions.

Can Climate Change Alone Explain these Results? Methods

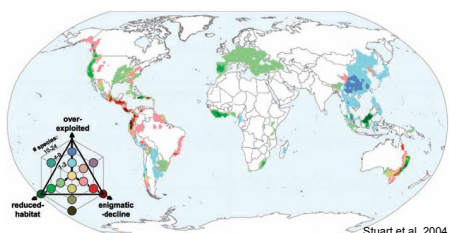
- Compared the magnitude of climate change and extinctions experienced by
 - *Atelopus*, believed to have been widely exposed to *Bd* and is found in a region where *Bd* has been detected as early 1894
 - amphibians in Madagascar, historically considered to be free of *Bd*
 - amphibians in Scandinavia, historically considered to be free of *Bd*

Can Climate Change Alone Cause the Declines? No!

An interaction between *Bd* and climate change seems to have caused the declines



Amphibians: The Most Threatened of All Vertebrate Taxa



What are the Greatest Threats to Aquatic and Amphibious Taxa?

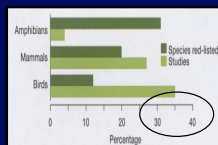
Answered by Wilcove & Master (2005)

- In US
 1. Habitat loss
 2. Pollution
 - Amphibian declines linked to upwind pesticide use (Davidson et al. 2001, 2002)
- Globally
 - Disease (Berger et al. 1998, Daszak et al. 1999)
 - Climate change?



Are We Adequately Addressing the Threat?

- 20-year report card on conservation science (Lawler et al. 2006)
 - Research on amphibians, pollution, climate change, and disease did not match the threat



Why Should We Care About Worldwide Amphibian Declines?

- Similarities between frog & human physiology
 - 1700 frog genes with human disease associations
- Ha in
- Me
-
- Important to food webs & ecosystem services
 - control insect pests that can spread disease; e.g. ticks, mosquitoes, flies
 - Amphibians account for more biomass in many NE forests than any other vertebrate