BI3294 - ECOLOGY II

19th Jan - Intro class

20/1/22

Complexity in Biology
Its because of -
- size & scale
- variation
- heterogenicity
- historical dependence

Modern definition of Ecology (Krebs 1972)
Ecology is the scientific study of processes regulating the distribution and abundance of organisms and the interactions among them, and the study of how these organisms in turn mediate the transport and transformation of energy and matter in the biosphere.

Scales ~~and~~ of pattern & processes in Ecology
Ranges from minitutes and mm (CO_2 exchange in leaves) ~~and~~ to thousands of years and kms (succession)
It also spans differrent levels of organisation.
Multiple components, stochasticity, emergent properties are some of the other things that lead to complexity in Ecology.

Problems and issues in ecology; and dealing with the complexity (Pigliucci 2002) Pg 6, Eco I

Framing and Testing hypothesis [Gotelli & Ellison 2004, Chapter 4]
Scientific Methodology
→ Deductive and Inductive reasoning
Both involve drawing inferences from data or models
* Deduction : proceeds from general to specific
* Inductive : proceeds from specific to general

Eg: Ants - Harvard Forest - Myrmica

②

Inductive reasoning

Popularised by Francis Bacon

Emphasizes link between data & theory

Builds upon previous hypotheses

Disadvantages : Single hypothesis ; problem of starting with wrong hypothesis

conventional inductive methods are based on data and doesn't include theoretical / abstract models

Hypothetico - deductive reasoning

Popularised by Karl Popper

- Forces to consider multiple (null & alternate) hypotheses simultaneously
- Highlights critical predictive differences b/w them
- Can be developed parallel to data collection
- Emphasis on falsification.

Scientific methodology - steps

Statistical Testing

Descriptive and Inferential statistics

This is a small part of scientific process. after experimentat-ion and data collection

Statistical vs Biological hypothesis

- Statistical hypothesis is one of 'no pattern'
- Rejecting stat. hypothesis can be different from rejecting biological hypothesis

P-value and significance

P-value is the probability that the observed difference will be found (by chance) if null hypothesis were true.

It serves as a guide to reject or not reject the null.

Its set at 0.05 (arbitrarily)

If p-value is large : observed pattern is likely because of inherent variation ⇒ don't reject null

small : implies difference b/w two groups is not because of random variation ⇒ Reject null

P value is determined by -

- Sample size (P ↓ with increase)
- Variation in the sample (P ↓ with decrease in variation)
- True difference between means (P ↓ with greater difference)

21/1/22

Lecture 3

Example of hypothesis testing

Ideal free distribution : individuals distribute themselves across several patches of resources to minimize resource competition and maximise fitness

Biological hypothesis

Hypothesis : Organisms adjust densities to match available resources.
Based on our current knowledge, we should expect that organisms would follow ideal free distribution
So our null hypothesis should be that population density would be positively correlated with resource availability.
Alternate hypothesis : There's no relationship between densities and resource availability.

Statistical testing – through experiments
* <u>Qualitative</u> : test if the mean density in high resource patch and low resource patch is different

* <u>Quantitative</u> : test of relation between availability & density where we have data for a range of patches.

Statistical null hypothesis is that there's no pattern
Qual null – no difference b/w means
Quant null – no correlation b/w availability & density
Statistical alternates : Qual – there's a difference b/w means
Quant – (positive) correlation b/w avail. and density

<u>Biological & Statistical hypothesis</u> <u>need</u> not match, they can be different.

With statistical hypothesis, you can either reject the null or fail to reject the null

27/1/22

Lecture 4

$p < 0.05$ – conservative level for rejecting null hypothesis

p value also represents the chance that we'll make a type I – falsely reject a true null hypothesis

But it still means that we need strong evidence to reject a null hypothesis

If we have a large enough sample size, then we'll find a bias in all coins.

false positive
Type I error - falsely rejecting a null hypothesis that is true
Type II error - failure to reject a null hypothesis that's false
false negative

28/1/22

Lecture 5

Framing and Testing hypothesis

Identity of Yeti - Lan et al.

They tested the bone, fur, teeth, skin etc samples and confirmed that all the samples came from known animals (bear, fox, dog..).

But does this mean Yeti doesn't exist?

"Absence of evidence is not evidence of absence) - Martin Rees

We can just say that based on evidence we have, we cannot say that Yeti exists.

Lady tasting tea - how p value came about

Null hypothesis - something that can be disproved in the course of experimentation.

If the odds of getting the result by chance alone (without an underlying reason) is < 5%, then it is accepted.

But this arbitrary cut-off is taken seriously and it actually takes away from important reasults

It's important to consider the context.

If we do 20 tests (with 20 colours of jelly beans), then by chance, we'd find that there is correlation b/w one colours and acne.

So if we're doing the same test n times, then we penalise it by lowering p value to 0.05/n

But what if this is an indication of how many studies w/ $p \geq 0.05$ we've missed out on?

Scary idea

* The reported studies seem to have greater frequency around (just below) 0.05, as compared to other p-values. (∃ publication bias, but idea of manipulation is frightening).

1/2/22

~~QUINN & DUNHAM [1983]~~

Strong Inference - Platt (1964)

↳ its a method of doing research which is systematically used and taught, an effective and accumulative method of inductive inference. It consists of applying the following steps formally, explicitly and regularly -

Definition *

1) Devising alternative hypotheses
2) Devising crucial experiments, with alternative possible outcomes that will mutually exclude one or more hypotheses
3) Carrying out the expt to get a clean result.

Repeat the steps, making subhypotheses or sequential hypotheses to define the possibilities that remain.

- Any conclusion that is not an exclusion is insecure and must be re-checked.
- Be "problem-oriented" not "method-oriented".
- Logic tree on a blackboard with possible controls & experiments
- Francis Bacon's Conditional Inductive Tree has been the basis of Strong Inference. Science advances by disproofs, not proofs, but disproof is a hard doctrine "So scientists are either soft-headed or disputatious."
- TC Chamberlin - "method of multiple hypotheses" - second important basis for strong inference
- Strong inference has been very effective in many disciplines of science. - provides a standard of maximum possible effectiveness.
- The Question : "What experiment could disprove your hypothesis?" or, "What hypothesis does your experiment disprove?"

→ THE EXCEPTION.

Questions -

1) How do evidences for evolution fit into this framework?
2) "except by eliminating all possible hypothesis" - how do we know all possible alternate ones?

Major beef → 3) No example or demonstration of how "strong inference" can be applied to an unsolved problem in ecology/evolution

6 QUINN & DUNHAM (1983)

- Ecological & evolutionary research has constraints that makes causes or relationships hard to disprove, so research is largely inductive
- Statistical testing involves working with predictors which are a proxy for underlying cause and we test how likely the result could've arisen from chance. This is different from Platt's 'strong inference'.
- It's hard to apply the methods of linear exclusion of hypotheses in complex systems of multiple causality. So, the point becomes to assign relative importances to the contribution of a number of processes.
- Three major problems –
  1. Usually, hypotheses can't be framed in a way that allows disproof of finite no. of discreet possibilities. – especially when processes vary over a continuum
  2. Contributing causes may have strong interactions among them. Univariate critical tests can't discern them.
  3. In practice, reliable null hypotheses are hard to construct
- Example of 1 : "competitive processes shape natural communities" – we can reject the null but not completely accept H1
- Biological methodology is more similar to statistical testing when it comes to additive interactions – requires multivariate experimental design and statistical analysis.
- Use non-interactive random models as null for interactive models to study natural communities. The reliability of estimates calculated from null models depends on being able to explicitly state the model.
- Examples of :-
  1. Non-alternative hypothesis – theories of plant succession
  2. Interaction b/w hypotheses – distribution of intertidal organisms
  3. "Null" hypothesis – it's v. hard to construct null models

  Detail?
- Controlled experiments are very useful, but ecology & evolution are not blessed with clearcut criteria for acceptance of theories. Formal method is a guide to innovation, however, not a requirement.

So, hypothetico-deductive method should be applied with skepticism in ecology & evolution.

3/2/22

Lecture 6

Platt 1964 paper

- Starts off with different disciplines are progressing at different rates – mol bio as compared to eco-evo.
  He says that Str. Inf. is not used regularly and insists that it should be consistently, repeatedly used

- Not all disciplines are the same, they need not have the same trajectories.
  - primary literature and knowledge that exists
  - the technology that exists allows us to ask different kinds of questions
  - practical constraints – time period, tractability, repeatability

For the discipline 3 things can hamper 'development' –

Bottlenecks at different stages
- information deficiency : this is early in the feild
- technical limitation
- theoretical / conceptual limits

4/2/22

Lecture 7

Quinn 1983 paper

- Alternate hypothesis may not always be mutually exclusive. Moreover, its not always possible for us to list all possible alternate hypothesis.
- There is still an insistence on use of Strong inference in complex feilds of ecology & evolution
- Popper – statistical tests are unfalsifiable – important pt. ~47 min
- There's some variation in Y that cannot be explained by X. that is bunched up as 'error'. Its not noise, rather it's probably because of deterministic processes that the experiment has not controlled for.

(8) Johnson 1999 8/2/22

Insignificance of Statistical significance tests

→ Common but supposedly incorrect interpretations of p-value –

- probability that results obtained were due to chance
- 1-P is considered ~~as~~ the reliability of the result – i.e. prob of getting the same result if the expt were repeated
- P value can be treated as the prob. that null hypothesis is true.

→ In reality, p value is Pr(obs or more extreme data | H_0) – probability of the observed data given that null hypothesis is true, the assumed model is correct and sampling was random.

→ P-value depends on results that were not obtained, and the intentions of the investigator, cuz that allows us to determine which outcomes of an expt. are more extreme than the observed one. ?

→ Point null hypotheses (which state that some parameters = 0 or some set of parameters are equal) are known to ~~bd~~ be false even before data collection.
This leads to 'gratuitous' significance testing.

→ p is a function of (1) difference b/w reality & null hypothesis
(2) the sample size.

So if sample size is too big, then there should be a penalty. (like dividing by $\sqrt{n/10}$).

The correct threshold of significance, P=0.05 is arbitrary

→ Usually, we don't accept null hypothesis but fail to reject it.
This can be due to lack of power (not sufficiently big sample size) or lack of effect (null hypothesis is actually true)

→ Power Analysis : recommended after getting non-significant result, to guard against wrongly declaring null hypothesis to be true

Its also used to calculate sample size needed to have a specified probability (power = 1-β) of declaring as significant (at α level) a particular effect (effect size).

Might be misleading – high p value will result in low estimated power, especially in retrospective analysis.

Problem

→ If an important biological difference doesn't produce significant result, then n is too small & researcher calls for further research.

→ Despite a lot of problems with hypothesis tests they're still used cuz they - appear to be objective, readily available & easily used, taught to students and possibly because of physics envy

→ 'Hard' sciences have scientific hypotheses that can be tested statistically. In 'soft' sciences, hypotheses don't come from theories, they are actually "statistical hypotheses" which are know a priori to be false. Scientific hyp are global (ie generalisable) whereas stat. hyp are local, applying to particular systems.

→ Replication of experiments is very important but very hard in ecology because it's hard to mimic all the conditions. Metaanalysis is useful but can be misleading because 'non-significant' results are less likely to be published

→ Alternatives to hypothesis testing and significance levels -

1. Estimates and confidence interval - CI provides both, an estimate of the effect size and a measure of its uncertainty. Author postulates that this is not in use cuz of historical reasons.
2. Statistical decision theory - theory of acting rationally wrt. anticipated gains and losses in the face of uncertainty. In ecology, type II (accepting false null) can be more costly.
3. Model Selection - acknowledge the uncertainty of model by considering various models
4. Bayesian approaches - for eg. we want to estimate a parameter θ

$$P(\theta \mid data) = \frac{P(data \mid \theta) \cdot P(\theta)}{P(data)}$$

Initial knowledge about θ $[P(\theta)]$ is modified by data obtained from study $P(data \mid \theta)$ to yeild find $P(\theta \mid data)$

Frequentist CI - if study were repeated infinite times, the CIs that resulted would contain θ 95% of the time

Bayesian → Credible interval - prob. that true value of interval lies within the interval is 95%

(10) Oksanen 2001 8/2/22

Is pseudoreplication a pseudoissue?

↳ stigmatizing label for experimental studies where inferential statistics have been used in the context of unreplicated or compound treatments.

Challenges Hurlbert 1984 papers on replication in ecology - but Oksanen says, some sacrifice scale to acheive replication, while others keep the scale & try to replicate as well as possible.

→ Trade-offs in large-scale systems: Its hard to study large scale dynamics with replicable experiments. Alternatives -

1 Microcosm experiments: Organisms are small, have fast dynamics and hence act as models of large scale systems.

They were used to disprove that competetive exclusion ~~can~~ doesn't (or rarely ever) cause discrete patches of vegetation.

Also used to corroborate exploitation ecosystem hypothesis (EEH) using protists & algae. But evidence from microcosms suggest that hypothesis is promising - more experimentation should be done large-scale ecosystems.

2. Focus on predictions on transient dynamics & individual behaviours.

? Eg: Greenhouse experiments - impact of voles on herb-rich boreal vegetation

But there's no guarantee for the existence of critical predictions referring to short-term dynamics.

3. Compare single treatment with replicated controls.

If cost of treatment is too high, have n replicated controls

We obtain (n-1) df which is better than just one.

Eg: Impact of predation on a coastal population of collared lemmings

We'd need to do some ecological reasoning, and connect the dots to arrive at the conclusion.

4. Conducting unreplicated experiment

If experiments are along major ecological gradients, then its hard to conduct replicated experiments.

4a Present results of unreplicated experiment without stat. inference

Alternate: Bayesian statistics - but it has subjective elements in the calculation of a priori probabilities.

→ How exactly?

In unreplicated expts, statistical inference ~~will~~ 'can only tell us there is a difference b/w groups', which would be obvious.

"But stats can also tell us how they're different : unnecessary lack of inf. stats is rudeness towards the reader."

4b. Pseudoreplication of the experiment

Without replication, its not possible to establish a statistical connection b/w treatment and its apparent effect

? Does this mean it'll just show variation, and we won't know, or won't be able to tell what it means?

Proposed method : • sequential point estimates of differences b/w the two statistical populations before & after the onset of the experiment.

• Compare CI of the two populations before and after, especially max estimate of pre-treatment to min estimate of post treatment.

$$p_o = 1 - (1 - p_v)(1 - p_1) = p_v + p_1 - p_v p_1$$

p_o : prob of getting observed difference if null hyp is true

p_v : prob as consequence of sampling, measurement error & random within-site variation (comes from inf. stat)

p_1 : prob that local factors, other than the treatment would account for the difference.

Its derived from biological reasoning.

When $p_1 = 0$, $p_o = p_v$ i.e. p_o comes from inf. stats.

Even without replication, inferential statistics gives the reader an idea about p_v.

Also, unreplicated expts provide material for sampling bias.

(12)

Epistemological dimension

- Compound treatments ~~are done so~~ are opposed because that statistically significant differences b/w treatment & control can emerge due to ~~uninde~~ unintended side effects of the treatment.
- There'll always be unwanted consequences : femo effect.
- Bayesian variant : emphasizes on corroboration of seemingly unlikely predictions

  Popperian variant : emphasizes falsification.
- Spontaneous experimental situations, without control, may arise but that doesn't mean they're not critical.
- The 'pseudoreplicated' experiments don't claim to have replications, and are designed & reported in agreement with basic principles of hypothetico-deductive science

  Their predictions are genuine, strong & less likely to have a priori corroboration.
- Criticism against Bayesian approach : Prob. of a hypothesis to be a perfect truth is always zero. But this needn't be true in ecological sciences
- Falsification perspective : Corroboration is considered only as by-product of an empirical test, & only falsification could teach us something new.
- Different ideas : Popper, Kuhn, Feyerabend, Lakatos

  Falsification ; Kuhn ↓ Empiricism ; Feyerabend : Consensus based ; Lakatos : Hierarchical structure of conjectures

9/2/22

Lecture 8

Oksanen 2001 paper

- Its a response to Hurlbert's paper.
- If there's just one control & one treatment, the difference b/w them could be just because of variation and not because of true difference b/w them.
- Pseudoreplication : using inferential statistics on replicates that are not statistically different i.e they are ~~different~~ dependent on each other.

  Eg. Studying colony morphology from same parent culture.

  Treating each cabbage in a plot as a replicate to study the effect of fertiliser.
- How to recognise replicates – identify the experimental unit.

  Growth chamber is the replicate, not the 50 plants growing inside it. Expt unit : smallest unit at which treatment is applied

Influential, ☆ Bookmark

I

10/2

Lecture 9

- Having multiple controls could also allow us to show that the treatment lies on an extreme position of the system
- Several unreplicated experiment could be included in metaanalysis
  - better for sampling bias and allocating funds.

[But metaanalysis itself could be biased because insignificant results are not published]

- At large scale, even unreplicated experiments could be informative when descriptive stats are used. Could lead to other studies.

Johnson 1999 paper

- 0.05 is an arbitrary threshold.
- Power analysis can be done either with some pilot expt to calculate the sample size, but if its done post hoc, then its not genuine

11/2/22

Lecture 10

- People just give p value — but its also important to know the sample size, effect size (difference b/w means) and the distribution of data points (if its bimodal, then our assumption of normality is violated).
- Akaike Information Criteria — helps predict the best model that explains the data

They work well when we have a lot of information/data, but doesn't use conceptual / theoretical hypotheses.

So these methods help in making initial jumps in a new field

→ Summary : 3 main problems

1. Conceptual issue : its hard to translate the classic framework to ecology — statistical vs null hypotheses, dependent Ha.
2. Statistical testing issue: Arbitrariness of p = 0.05, sample size & scale, assumption of normality, interdependence of data, pseudoreplicatn
3. Practical constraints — Scale, stochasticity, other logistic problems.

(M)

Lecture 11
Biodiversity

Latitudinal diversity gradient

Diversity of various taxa (trees, fish, ants etc) decreases as we move from equator to the poles. This is true for all taxa except some.

Recognized early by Wallace 1878 & described by Dobzhansky, Fisher & Pianka in 1950.

- Exceptions

This happens when some taxa are more adapted to certain climate, or they have high dispersal / migration

Eg. Migratory birds, conifers, coastal organisms

Other possible explanations

- Incomplete / restricted scale of sampling
- Climate buffering in coasts
- Highly specialised taxa

- Why this pattern of biodiversity?

There's no agreement on underlying mechanisms.

Gaston 2000 – perhaps a single hypothesis doesn't explain it.

Rhode 1992 – 28 hypotheses were listed :-

* 12 of these were circular : eg. greater predation/competition in tropics
* 11 based on insufficient evidence
* 5 based on time – tropics have had longer time of constant climate for organisms to evolve

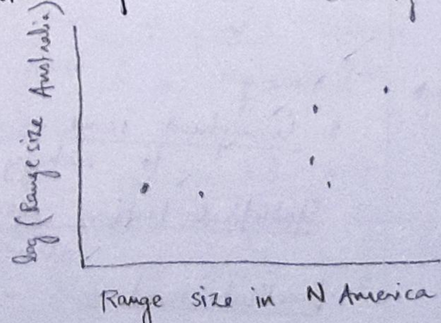
- Main hypotheses

1) Area constraints : Larger land mass will be able to sustain ~~Energy to~~ larger species diversity, because they can sustain larger population and hence lower level of extinction.

This allows for greater allopatric speciation because more genetic diversity

Species area curves

Some correlation



Allopatric : geographically isolated

* Mid-domain effect

2) Energy hypotheses

Increased solar radiation (even temp and water) at tropics → Greater primary productivity → greater no. of species

↳ greater pop. density & ~~faster gen. time~~ → lower extinction rate

Also higher T → more metabolic rate (short gen time) → faster speciation rate

Lower ext. and faster speciation rates lead to greater biodiversity in the tropics

But there is little empirical evidence for increase in no. of individuals with latitude

3) Climate

* Climate harshness : fewer species can withstand harsher climates
* Climate fluctuation / stability : tropics are mild & stable over long temporal timescales. Fluctuation increases extinction rates, which doesn't allow specialization in temperate zone.

4) Evolutionary history

- Historical perturbations
  Not sufficient time for speciation in temperate zones.
  Eg. due to glaciation cycles.
- Evolutionary rate
  High T → high mutation rate → short gen time → high speciation rate
  There's some empirical evidence for greater microevolutionary rates in the tropics, but what about extinction rates?
- Together, these two explanations gives the evolutionary history hypothesis

5) Biotic interactions

This is a circular argument - you need more species in the first place to have many biotic interactions.

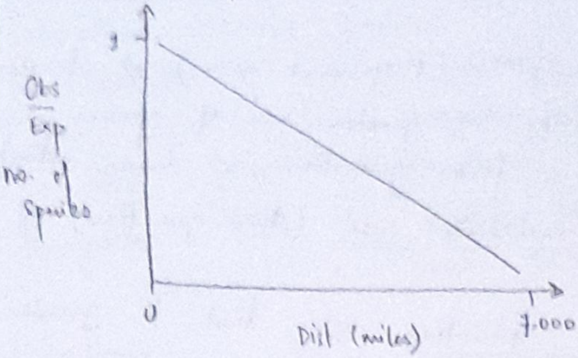
(16)

Lecture 12

17/3/22

Island Biogeography

Exp → expected no of species near mainland



Ratio of $\frac{\text{obs}}{\text{exp}}$ number of species declines with distance from New Guinea.

Further away you're from mainland, harder it is for species to disperse to the island

Robert MacArthur and E.O Wilson

Proposed a hypothesis to explain pattern of species richness on islands.

Equilibrium theory proposes that no. of species is determined by rate of incoming species and rate of local extinction on the island. They are mainly determined by —

1) Size of island : large size → supports larger population → lower level of extinction
2) Distance from mainland : decides colonization rate by new species.

This theory can also be applied to sky islands (eg. Shola grasslands — occur only above certain elevation), conservation and other systems.

Species - Area Curve

Thought expt : How does the no. of species increases as we increases the area of sampling space ?

60 man hrs — Say 10 people go to a place for a day (→ 10 hrs) : exp no. of birds = 20

600 man hrs — If they go for 10 days continuously = more birds : upto 40

1 man hour — If one person goes and observes for one hour :

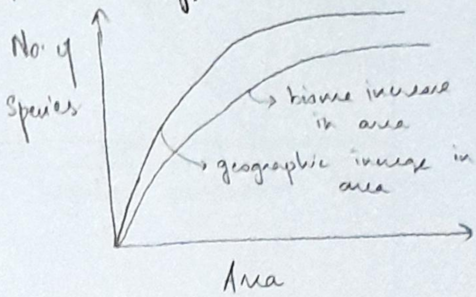
With increased effort, no. of observed bird species increases, but after a point, it plateaus.

If they are observed through the year, no. of observed birds will increase, because of migrations & so on.

If we keep extending the sampling area, sample more locations, then no. of birds observed will increase.

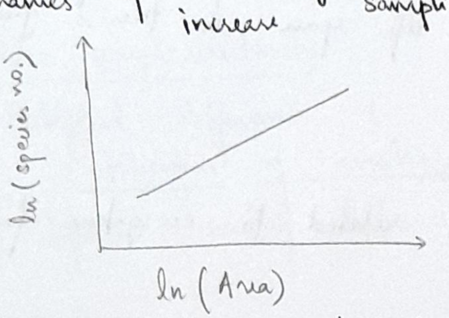
But it need not be a monotonous or linear trend.

Even if we're extending sampling effort in the same biome (savanna), the no. of species (cumulatively) increases.



If we increased the sampling area from a geographic point, then we'll be including new kinds of habitats, so the rate of observing species will be higher.

Why this pattern?
- Larger area supports larger population ⇒ more no. of species
- As size increases, we include new habitats & new niches, so we observe more species
- Chances of observing rarer species increases as we increase sampling size.



$S = cA^z$ equation

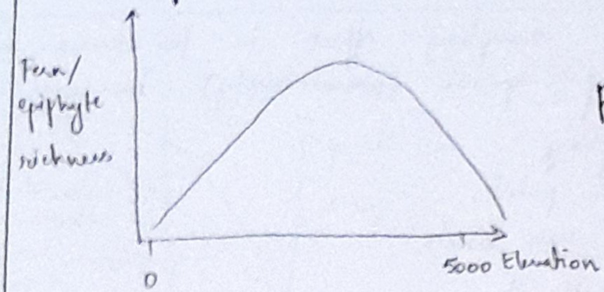
Area constrains the no. of species that can be present.
Species-Area curve: important to explain biodiversity patterns.

18/2

Lecture
Latitudinal gradient of diversity explained by thinking of tropics as – Cradle: sustaining greater no. of species
Museum:
Out of tropics model:

5. Biotic interactions
Results in increased specialization ⇒ greater coexistence of species
Why greater biotic interactions in the tropics?
Circular argument, plus no empirical evidence – studies fail to ~~go~~ record increased biotic int. in the tropics

Similar to latitudinal gradient, gradient along elevation and depth are similar – diversity decreases monotonously (usually)



Mid-domain effect

For some taxa, species diversity increases and then decreases with elevation/depth

Null hypotheses: because of geographical constraints, but there other hypotheses

Mountain passes are higher in the tropics as compared to temperate mountains ⇒ Tropical mountains are more separated

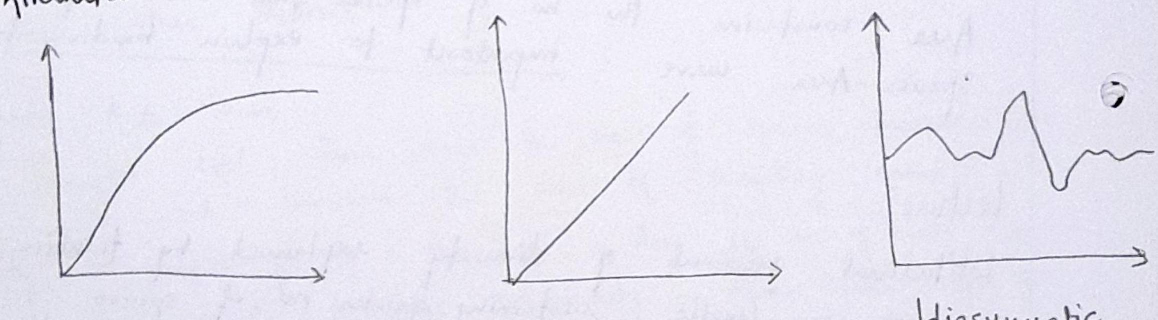
Temperate organisms have greater tolerance range and therefore elevational ranges and dispersal ability.

Similar pattern in marine animals: temperate organisms have greater tolerance & longer life span so there's greater dispersal

Biodiversity and Ecosystem function

Null: ecosystem fn is not related to ecosystem function

Alternates –



Redundant Linear Idiosyncratic

Linear increase ⇒ all species contribute to function in a similar way. Conserving all species becomes important

Redundant: Beyond a critical level, adding more species becomes redundant, doesn't increase function

Tilman et. al ⇒ protecting/conserving key species becomes important

Idiosyncratic: unpredictable relationship.

23/2/22

Lecture

Processes that may explain relationship b/w diversity & ecosystem

1 Sampling effect (Portfolio effect)

More diverse communities have greater prob. of containing and becoming dominated by a highly productive species.

Eg. Tilman et al.

Portfolio effect – if species fluctuate independently, but their cumulative biomass may not fluctuate that much.

⇒ more diverse communities may have lower variability

Important for resilience / recovery from disturbance

2. Niche complementarity

Ecological differences b/w species leads to more complete utilisation of available resources in more diverse communities.

Eg: different rooting depths in prairie grasses

3. Mutualisms

Increase in mutualistic interactions among species in more species rich communities.

Eg: N_2 fixers enrich soil nutrients & allow other species to increase productivity.

Criticisms of Biodiversity-Ecosystem Function (BEF)

Recall: Eco I Cardinale et. al. (pg. 78)

- They compared productivity of monocultures to polyculture. Polyculture was better than average of monocultures, but most productive monoculture is sometimes better / or not very different from diverse polyculture

- All BEF expts are in small, homogenous mesocosms, but the real world might be different

- Most BEF expts are also random-loss. But we know extinctions aren't random.

Cardinale et al also found that the BEF effect increased when scale of experiment increases.

Species extinction is not random. Vulnerable species –
- smaller populations / restricted range
- specialists
- higher trophic levels / larger animals are more likely to go extinct

Conserving most prod. species is not a good idea
- It might not remain the most productive fo species – it maybe vulnerable to some ~~con~~ changes in environment
- We'd also lose out on interactions between other species
- Ethical and aesthetic reasons
- Evolutionary capital

24/2

Lecture

Ecosystem functions

Biological processes that involve flow of energy and nutrients in, out and through food webs

Functions that benefit humans are called ecosystem services.

- Carbon fixation	- Pollination	- Biomass prod^{n}
- Soil formation	- Decomposition	- N_2 fixation
- Water purification	- pest suppression	- Energy flow

Constanza et. al. 1997 – cost of ecosystem services : 33.3 trillion \$
Total global GNP (1997) ~ 18 trillion \$

Threats to biodiversity
- Habitat destruction & degradation (for agriculture & pastoral land)
- Overexploitation (fishing, hunting)
- Pollution (domestic & industrial emmission)
- Global climate change (Greenhouse effect, ozone layer destruction)
- Invasion by introduced species

Several species have already gone extinct & many others endangered
20 - 30% of vertebrates are endangered
35% of mangrove habitat, 50% hard coral and ~ 200,000 sq miles
of Amazon have been destroyed

3 species (rice, wheat, grain corn) provide 60% of calories in our
diet → 75% of genetic diversity has been lost.

Since rise of humans, 83% of wild mammals, 80% of marine
mammals, 50% of plants & 15% of fish have gone
extinct.

Humans and Net primary Productivity
Humans use / waste / destroy about 27% of world's NPP &
40% terrestrial NPP.
Vitousek et al ; Bar-on et al.

Distant past - < 1 mammal went extinct every millenium
(from fossil record)
Recent past - 1000 x times more than fossil record
Future (modeled) - 10 x more than current

1/3/22

Lecture 16 - 25th Feb

Tilman et al 1996 - experimentally showed that total plant
cover increased and Nitrogen leaching in soil decreased
with increasing species richness.
This could be just because of including the 'most productive
species' as you increase no. of species in the experiment.
Underlying mechanisms - (that can explain the correlation)
- Niche complementarity
- Sampling effect
- Mutualistic interactions

Measures of diversity

Indices of diversity takes in numbers of species & their abundance

Most studies / measures just consider species number, but is it enough?

Could it be a function of species productivity & species no.
But it hard to do that.

Can we measure diversity at a level above species?

- Phenotypic diversity – phenotype ultimately contributes to function
  for instance, consider maximum size / size classes of individuals plants rather than no. of species
  Classify bacteria by the carbon source they can digest rather than no. of species in a community.

- Genetic diversity
- Functional diversity – focus on functional attributes of species
  Same as phenotypic diversity?

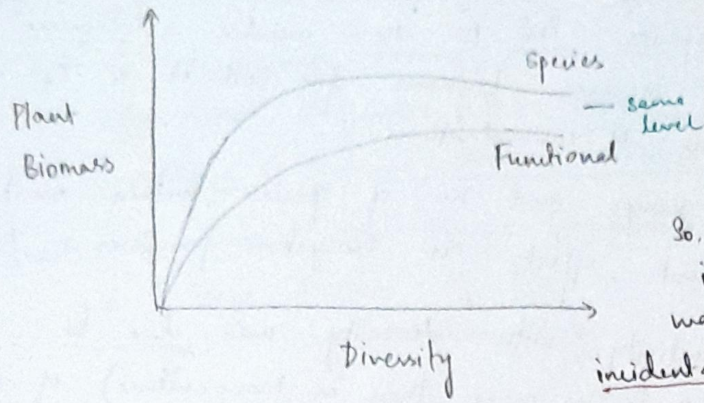
This can takes us from measures of diversity to measure of ecosystem function.

How could we extend Tilman's study?
We could perhaps start by measuring the niche use of each species. We usually use traits as a proxy for niche use (root length – soil level usage) and trait similarity to study niche overlap

If we take functional groups on X-axis and plant biomass on Y-axis, the increase in ecosystem fn won't be steep & larger plateau

Functional groups –

- Legumes : fix soil N_2
- C_3 grasses : grow better during cool seasons
- C_4 grasses : —— " —— hot season
- Woody plants : allocate more carbon to branches, long lived
- Forbs : High allocation to seeds, don't fix N_2



The rate of increase with increase in functional diversity is lesser than the earlier rate.

So, perhaps the ~~up~~ steep increase due to species increase was because they also incidentally increased functional diversity

Hooper & Vitousek – "Differences in plant composition explained more of the variation in production and N_2 dynamics than did no. of functional groups present."

1/3

Influence of functional diversity & ~~processes~~ composition on ecosystem processes. – Tilman 1997

- Species diversity (no. of species), functional diversity and functional composition (which fn. groups were added) were varied in experimental set ups.

Groups : legumes, C_3 grasses, C_4 grasses, Woody plants, Forbs

- Response variables –

Productivity	Plant % N	Plant total N ↑
Soil NH_4	Soil NO_3	Light penetration ↓

In multiple regressions with these variables, functional diversity was significant in all 6 cases whereas species diversity was not. (for multiple regression, not univariate regression)

- Thus, functional group component is a greater determinent of ecosystem processes.
- Soil NH_4 and NO_3 levels didn't depend (significantly) on functional composition. 4 other variables were significantly impacted by functional diversity & composition (by one method of testing)

(24)

- Species & fn diversity explains 8% of variance whereas functional div & composition explains 37%
- C_4 grasses and legumes significantly affected productivity. Presence of C_4 grass species led to 90% increase & legume species led of 59% increase. Legumes fix soil N & C_4 grasses lower tissue N concentrations.
- Presence of fn groups and no. of species within most fn groups had significant effects on ecosystem processes
- Increase in productivity with diversity was due to overyielding (producing more than in monoculture) of species, especially C_4 grasses (14 out of 34). Whereas only 4/34 underyielded → most plants inhibited themselves in monoculture i.e high intraspecific competition.

Mechanism

- Species & functional diversity are correlated. both give significant results, but functional diversity / composition has greater impact

Loss or addition of certain species has greater impact on particular ecosystem processes than other species.

1/3/22

Effects of Plant Composition & Diversity on Ecosystem Processes
Hooper & Vitousek 1997

Ultimately: Plant composition more important than no. of fn groups present
Could be because of Niche complementarity or Portfolio effect

Response variables: Productivity, N-leaching losses, Resource Availability

Functional groups:
- Early season annual forbs (E)
- Late season annual forbs (L)
- Perennial bunchgrasses (P)
- Nitrogen fixers (N)

Groups differ by phenology & characteristics important for nutrient cycling (root depth, root-to-shoot ratio, size, foliage, C/N ratio)

- Biomass DID NOT correlate with increasing functional group richness. Rather, treatments having same no. of fn. groups showed significant difference in response variables.
  ⇒ Composition explains more variance than richness.
- Traits of certain fn. groups (competetiveness of E's & L's in mixture, and large biomass of P's in monoculture) had greater impact than complementarity.
- E's alone depleted N in soil more than other groups, and any functional group with E's had low soil N level (supports R^* hypothesis)

Under what conditions can they coexist?

Intra/intersp. compt.

- Testing N-retention by adding tracer - how?
  Most N's was recovered from the soil
  * N-Retention wasn't significantly affected by fn. groups
  * Bare plot had the lowest N-retention.
  * "In short term, microbial immobilisation is a more important pathway for N retention than plant uptake
  * Here too composition ≫ richness
- Differences in Species composition & diff. in species richness can be correlated. So, we need to consider species & functional groups grown alone & in more diverse combinations to understand mechanisms of diversity effects on ecosystem processes.
- This becomes important for agriculture & land management

2/3/22

Lecture 17

Biological mechanisms that leads to increased diversity resulting in better ecosystem function -

- Niche complementarity
- Facilitation : an interaction where one or two species benefit from the interaction.
  Eg: Nurse plants - colonizers in desert or high altitude areas which makes in easier for other plants to grow in the vicinity

(26) - Relation b/w functional groups — traits, niche, interactions
Traits are more similar b/w individuals in the same functional group rather than across traits. So, different groups occupy different niches, so lesser competition

- Overall, both species and functional diversity (r^2) contribute to ecosystem function. But in multivariate regression, they found that species diversity is not significant. The earlier result of sp. div with ecosystem function was because sp. div and functional diversity are correlated.

- Functional composition — i.e species identity in the ecosystem also plays a role

3/3

Tilman et al 2014 (Review)

→ Elton (1958) after qualitative observations that increasing biodiversity increased stability, resilience & productivity

1970s : May's theory (1973) predicted that population stability was lower when biodiversity was higher.

For randomised interaction

Eltonian → Individualistic paradigm: few dominant species determine ecosystem processes.

→ Re-awakening
In 1990s, calls for conservation & shift towards answering questions through experiments —
1. Are diversity effects real?
2. Underlying mechanisms
3. How general are these effects?
4. How important are they?

→ Advent of field experiments : Tilman 1996
- Increased biodiversity → ↑ plant cover, ↓ soil N leaching
- Other studies found more significant correlations with functional diversity and composition. (Tilman 1997, Hooper 1997)
- Hector 1999 — study sites across Europe — generalised the results.

→ Causes of Biodiversity effects

Inferred that greater trait diversity was the direct cause, but Huston (1997) questioned this & said the results could be caused by 'Hidden treatments' (?). Others found/insisted that environmental factors were more important, or it could be due to statistical averaging

3/3/22

Lecture 18

Hooper paper

Study was done in reclaimed serpentine grasslands (greater heavy metal conc?)

- There is a decrease in # inorganic N in soil decreased with increase in functional group richness (1c)
- In general there's no correlation b/w biomass and no. of fn groups But when E is included in the functional group, there's an increase in biomass increase
- Biomass production of monocultures : P > N ~ L > E

  P > ELPN > ELP > EP

Productivity of – all monocultures averaged ~ 200 g/m²
most productive polyculture ~ 200 g/m²

~ 34 mins – something about statistical artefact

Multitrophic studies are important, also some plants could be better than others at braving some stresses

Assumption of equilibrium may not be true

4/3/22

Lecture 19

23/3

Lecture 20

BEF effects seem to be general (Cardinale et al)

Non-random removal of species

Experimental studies remove species randomly from random combination / assemblage of species. So what does it mean for inferring the results of these studies?

- Design experiments based on realistic combination of species and extinctions – The results still hold

Species with overlapping niches are less likely to coexist in nature, further interactions (mutualism etc) can shape community composition

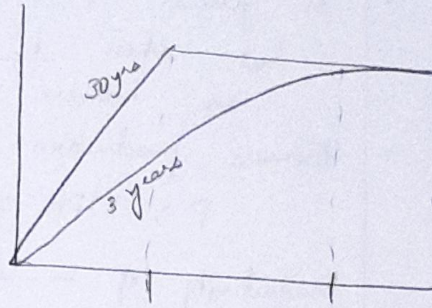
- Also, when niches overlap, there is resource partitioning and character displacement.

30 Factors that affect species loss — how are they related to BEF?

Say, the two most productive species don't occur together in nature — it's important to study non-random assemblages and non-random loss of species over time.

Some final results —

- The species no & ecosystem function are positively correlated and ecosystem function increases and then saturates at high sp. no.
- Over time, the relationship becomes linear initially, and function saturates at earlier species no.



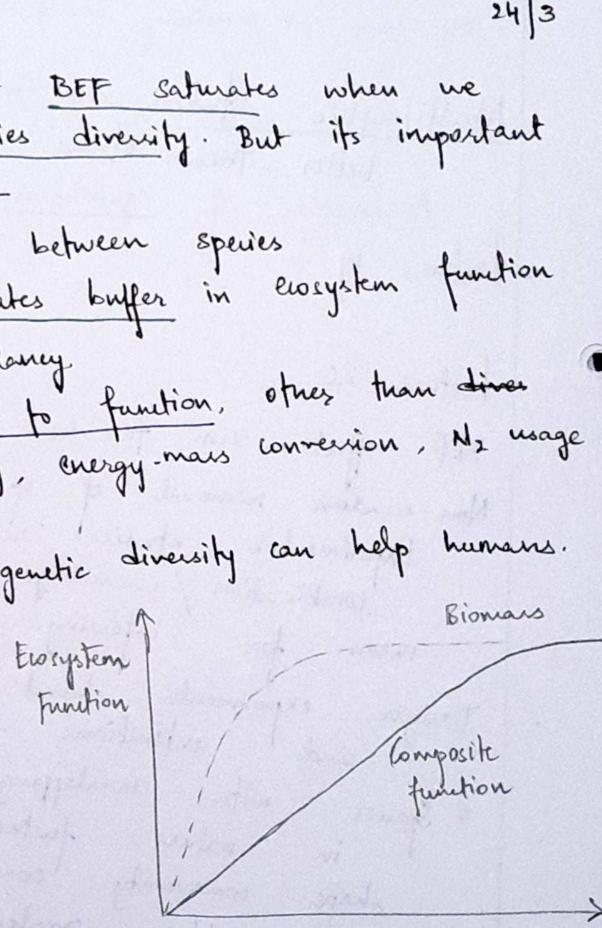
Lecture

24/3

These studies indicate that BEF saturates when we have 20-25% of species diversity. But its important to conserve all species —

- Sensitive biotic interactions between species
- Having multiple species creates buffer in ecosystem function because of redundancy.
- There are many dimensions to function, other than ~~dives~~ productivity — stability, energy-mass conversion, N_2 usage and so on.
- Evolutionary potential — the genetic diversity can help humans.

The rank of species won't stay the same with changing biotic and abiotic conditions.



Final questions / comments

1. How can we translate this result to large habitats?
We'll need greater sp. diversity to maintain function.

2. Multi-trophic level and complexity - roughly same relations still hold

3. How does destruction & degradation affect BEF?

Caveat: Observational studies show conflicting results - some positive, often no relation and sometimes even negative relationships.

Limitations in experimental conditions -

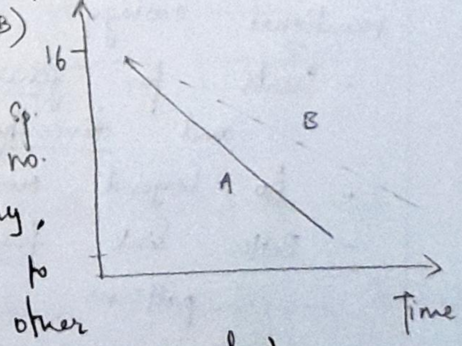
* Spatial and temporal limitations
* Too controlled - no seed influx, recolonization
* Can't observe evolutionary changes / genetic drift → not imp. for ecological studies
* Random assemblages and ~~non~~ random extinctions.
* Assumption that the system is in equilibrium.

Crawford paper

If the system is not in equilibrium, how will it change?
In a 3 x 3 m plot, if 24 species are planted, the sp. number will decrease over time.

If we have a plot with most productive 16 species (A) vs least productive 16 species. (B)

the rate of decline would be faster in A.



More productive plants grow rapidly, use resources more efficiently & to a better R^* value, overshadow other plants & so on - so species decline is faster.

Niche complementarity also plays a role in deciding slopes of A & B.

Lecture

Functional Ecology / Trait based Ecology

Lawton 1999 : Are there general laws in ecology?

Simberloff 2004 : Community Ecology : Is it time to move on?

It seemed that ecological patterns, rules & mechanisms that underpin them are contingent on organisms & their environment.

This contingency is manageable at individual & very large scales (ecosystem / biome). But it becomes overwhelmingly complex at intermediate scales i.e. community ecology.

It seems hard to come up with general laws or patterns.

We study different things across different biological scales.

When we measure biodiversity as sp no. and compare how biodiversity varies, we are giving each species equal weightage and losing out on functional attributes. eco function

This is a problem in community / ecosystem studies.

Later Tilman & Hooper papers use functional groups to study how ecosystem function varies. These groups occupy different functional niches

Functional ecology

- Search for general principles that simplify complexity and diversity of ecosystems. (Calow)
- Go beyond ~~easy~~ taxanomic identity
- Better link functional traits - environmental gradients - patterns in ecology.

Functional groups : related organisms with similar properties.

Eg: Pioneer vs. Climax species ; r vs k strategists.

But there was still some frustration with defining & linking categories, and it still becomes qualitative.

Trait based approaches are – more quantifative, closely related to performance, which gives us better predictive power and scales well across different biological levels.

Approaches are being used in studies in –
physiology : integrated phenotype. relationship w/ env.
population biology & sp. interactions
community ecology – assembly rules
ecosystem – ecosystem function (energy flux, CO_2 fixation).
evolutionary dynamics.

Allows seamless scaling from organisms to ecosystems
....

What is a trait?
A measurable (quantifiable) attribute of phenotype – can be morphological, physiological or phenological & behavioural.
Functional trait – a trait that is closely related to function (performance, demography. growth, rep. fitness).

Plant tissue traits –
- determine interaction w/ environment & hence distribution across geography
- define habitat and resources for other organisms
- influence ecosystem functions, processes & properties.

Areas of research
1. Integrated phenotypes – how are traits related to each other and to performance
2. Life history and ecological strategies – quantifying diversity of strategies
3. Community structure and composition
4. Quantifying ecosystem function
5. Evolutionary dynamics.

Individual traits → performance ⇒ Demographic/Population traits ⇒ Community/Response traits ⇒ Communities + Abiotic factors ↓ Effects traits

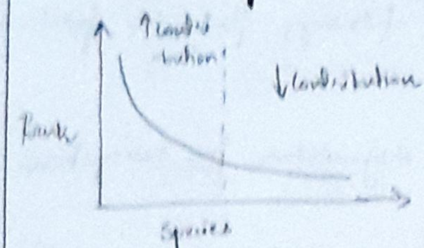
30/8

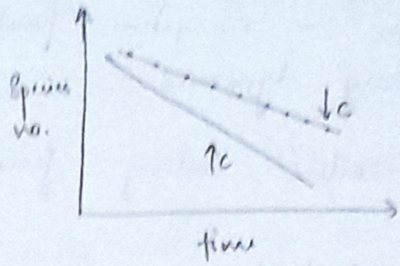
Lecture

→ Crawford et al 2021 Paper discussion

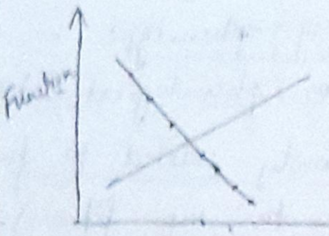
function dominance correlation : How is the contribution to function related with dominance of species. They contribute more to biomass → they are superior competitors, so they're dominant species

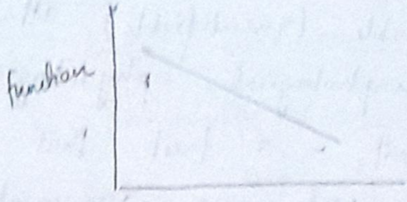
baseline capacity to contribute to ecosystem function





Counter gradient : variation in BEF lines





↳ how much they can outcompete other species

Based on dominance, very high species no. will decrease in species number, while function remains high because dominant species remain.

This would explain the neutral or negative results observed in various studies.

→ Hagan et al 2021

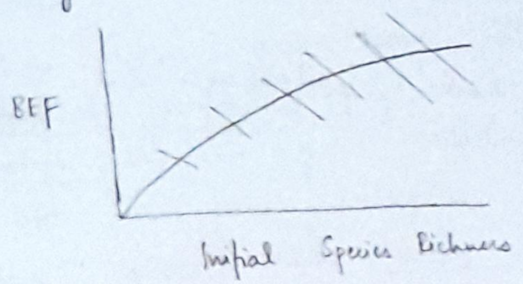
They reanalyse previous data based on the earlier premise.

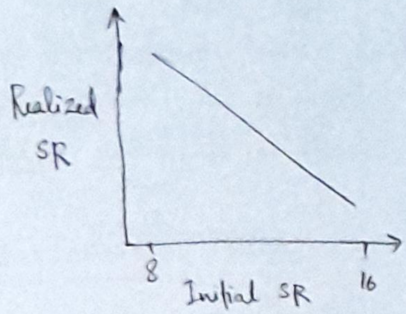
Different scales: Local
Regional
Landscape/Biome
Continental
Global

Not much species loss is happening at local scale, but we study BEF at local scale

Lecture

Something in the Crawford paper





If there are more dominant species in the initial mix, then the realized SR is lesser

Hagan paper

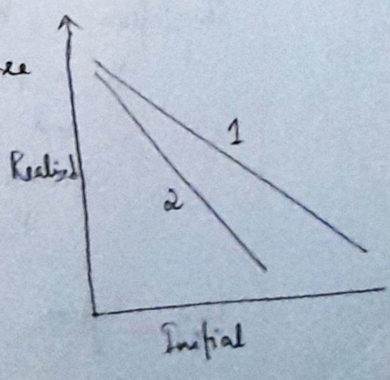
Premis
- A lot of field studies show variable results
- In local scale, there's no species extinction - its happening at the regional / global level
- There seems to be +ve relation at local scale, but neutral or negative relation at larger scales.

It tries to explain why this might be, and reanalyse data. 3 mechanisms -

1. Niche complementarity
2. Selection effects
3. Facilitation — not v. important.

If BEF is mainly due to complementarity, then the decrease to realised SR is going to be small - because species can coexist better

If selection effects are strong, we'll see large decay going from initial to realised SR



But we don't have a good idea of their relative contribution.

If NC is important, we'd expect the same positive-saturating relation b/w realised SR & BEF.

If selection effects are important, we can get results on negative effects.

Can we talk about initial sp pool and based on current sp pool?

This paper doesn't include composition - BEF at local level and whether it can be applied to conservation?

Schnabel paper

Diversity increases stability in grasslands, but forests are different - they invest in more long lasting structures and changes occur more slowly.

Mechanisms behind diversity - stability - 2 reasons.

They measured temporal variation in mean & std. dev. of productivity. Measure of stability : $\boxed{\frac{\mu}{\text{std. dev}}}$

It measures whether you're productive consistently.

If there's too much variability, then std dev would be high.

$\frac{\mu}{\sigma}$ for each species

Mechanisms -

1. Asynchronous species growth

2. Population level stability

1/4/22

Robert May - theoretically, for random aggregations, increased sp richness decreased species stability. contradictory to some data

Drought resistance traits - stomatal control and cavitation

Cavitation : When vapor pressure deficit is high & the soil dry, the tension in string of water in xylem increases, and ~~water~~ air bubbles are formed, and they're often irreversible.

Ψ_{50} - how much -ve water pressure can a plant withstand before 50% of xylem is cavitated

Large xylem ⇒ more susceptible to cavitation

Species richness may increase community stability indirectly via promoting asynchrony through ~~fn.~~ diversity in traits (37)

Water spenders: ↓ drought resistance ↑ water use ↓ stomatal control
The converse is true for water savers.

Deciduous species drop leaves because they don't have good stomatal control, they have large xylem → acquisitive strategy ie can grow rapidly when water is available, but its more susceptible.

Evergreen species have better stomatal control and conservative strategies.

How do species-level traits affect population stability?

Result: Increased asynchrony increases stability
No relation b/w population-level stability & overall stability

Community weighted-means: we weigh the mean value of each species by their dominance
Related to even-ness of species distribution – CWM is value modulated by the proportion (by abundance or size) to get an integrated trait value for the community

6/5

Lecture

Community composition and structure

Studies examining environmental drivers of community composition and structure are hard to generalise

---

// Biomass, reproduction & survival are measures of performance in different conditions, when combined, they give the fitness of the individual

38

Assembly rules

- Habitat filtering : Dispersal range, Overlap with fundamental niche, Biotic interactions

- Limiting similarity / Niche partitioning through trait divergence

How to correlate these processes with traits?
It requires an understanding of how trait combinations respond to environment, how they're related to performance, intraspecific variation in species.

Hierarchal perspective

Batholemew - each level finds its explanations of mechanism in the levels below and its significance in the levels above

Kingsolver & Huey (2003) -
Performance is fundamental to biology. Understanding how lower level physiological, morphological and behavioural traits determine performance in various environments.

Jung et al: Including intraspecific variation improved the understanding of habitat filtering & niche differentiation

Leaf functional traits
↳ Primary photosynthetic organ. Leaf traits are good indicator of productivity, and in turn fitness.
We don't know well how leaf traits are related to each other.
- Constraints, pliedropy, genetic linkage, correlated selection * problems with traits
. defines plant interaction w/ environment, allows us to understand plant distribution, defines habitat for others

People prefer dry weight — because water content can vary during the day

Key Leaf Functional Traits —

Most important 6 traits
- Assimilation rate (A_{max})
- N_2 conc (N)
- Leaf mass per area (LMA)
- Leaf lifespan (LL)
- Dark respiration rate (R_d)
- Phosphorus conc (P)

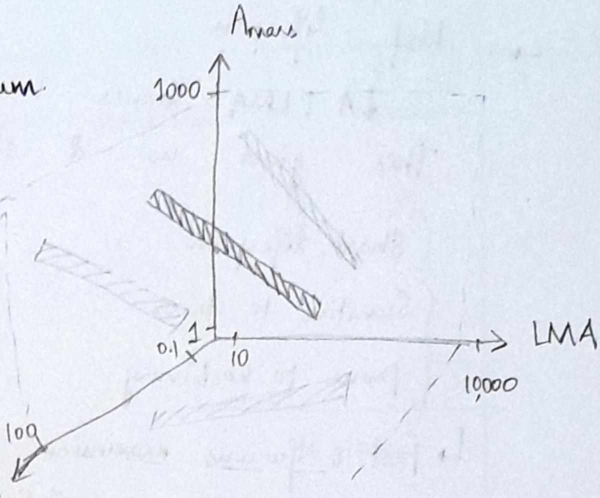
Less important
- Relative water content (RWC)
- Water use efficiency (WUE)
- Potassium conc (K)
- Nitrogen use efficiency (NUE)
- Carbon : Nitrogen Ratio (C:N)
- Nitrogen : Phosphorus Ratio (N:P)

Worldwide Leaf economic spectrum

Wright et al — ~2500 species

In LMA, most major component is Carbon. As LMA increases, there's already more carbon per unit area.

So the tradeoff is thin leaf - large area or thick-leaf and small area



* LMA - A_{mass} : Negative

N - A_{mass} : Positive *

* LMA - N : Negative

↳ thicker leaves have less N

This is true for all plants, in general

7/4/22

Lecture

PCA : Principal Component Analysis

↳ a method to reduce dimensionality in a multivariable dataset such that spread of points is maximised.

differences in datapoints

With PCA, you can keep collapsing dimensions with least variability

40

What they found is the observation of 3 variables in 3 dimensions from 12 dimensions.

→ These variables are correlated with each other

Along the axis, the species go from

long-lasting leaves	↓ A_{max}	to	↑ A_{max}	juicy leaves with ↑ N that photosynthesize more
	↓ N		↑ N	
	↑ LMA		↓ LMA	

This is the leaf economic spectrum

→ leaf lifespan

↓A ↑LMA leaves have longer lifespan than ↑A ↓LMA

This gives us 2 strategies –

- Short lifespan
- Sensitive to stress
- Prone to herbivory

↳ fast & furious maximise returns & carbon assimilation

- Long lifespan
- Stress resistant
- Resistant to herbivory

↳ Slow & steady maximize persistence & longevity

LMA correlates with these strategies.

Diaz et al – Global spectrum of plant form & function

They considered key leaf traits and other traits – seed mass, plant height, wood density etc.

- Trait space actually occupied is restricted
- Plant species largely occupy a plane (75% variation)

Two key traits –

- Size of organ (seed mass, height, leaf area)
- Leaf economic spectrum (LMA, N, A_{mass})

Other axes that emerged -

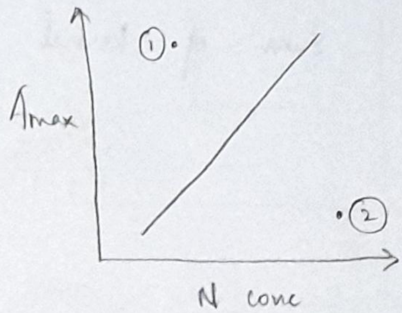
1. Seed mass & plant height are highly correlated
2. Seed mass & Nitrogen content are orthogonal axes ⇒ they are uncorrelated

There's also a lot of blank space - some trait combinations are non-viable (1) or non-selected (2)

Also, species exist on the map as two clusters.

(1) • Some trait combinations cannot exist - physiologically impossible

(2) • Some trait combinations are selected out because they don't do well



The two clusters are -

- herbaceous plants
- trees

They vary along size.

Other clusters represent lower plants, gymnosperms and angiosperms. You can ~~&~~ also map evolution of different groups.

8/4/22

Lecture

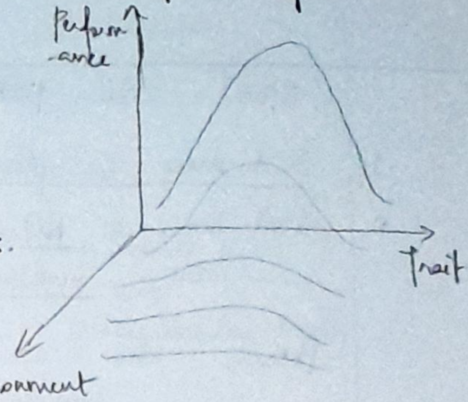
How to move from functional traits to habitat filtering?

We know how traits relate with each other. We need to connect traits to performance.

We're not considering how traits change because of environment - plasticity cause intraspecific variation which is very small compared to interspecific variation; and evolution occurs at different timescale.

But fitness / performance of traits is defined for a particular environment.

Traits are a <u>proxy for niche</u>

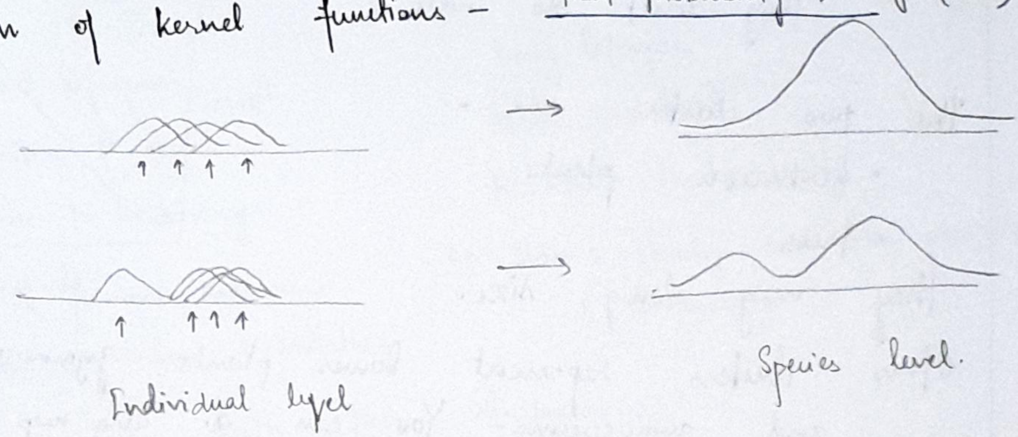


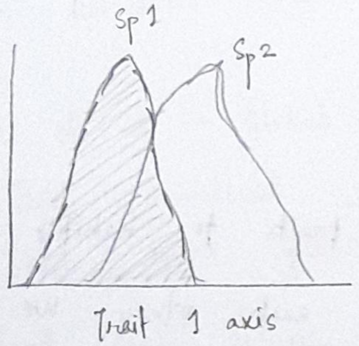
We need to understand how the performance of trait combinations changes across different environments.

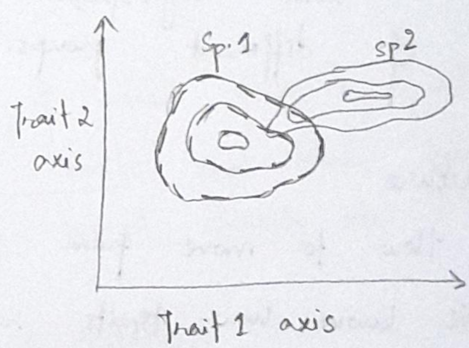
Tilman et al chose to measure nitrogen cycling because N is the limiting factor.

Say, we have some understanding of how traits correlate with environment.

Sum of kernel functions — <u>Trait Probability Density (TPD)</u>







We can integrate species' TPD to <u>community</u> and <u>regional TPD</u>, and compare across communities which can let us infer certain properties.

Eg. Measuring LMA at community can tell us about environmental factors, N content, leaf lifespan and turnover herbivory.

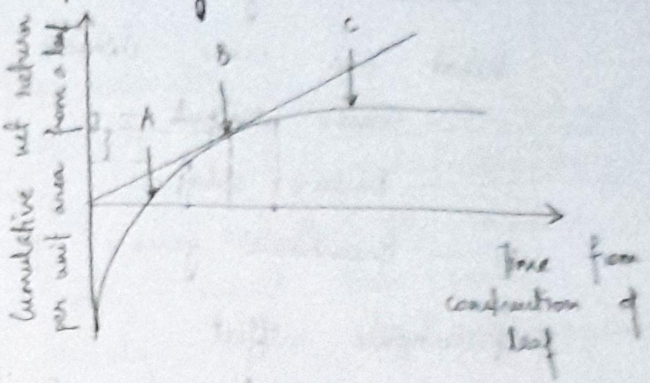
Lecture

Westoby paper discussion

- They look at 4 dimensions of functional traits – LMA, seedmass & seed output, leafsize twigsize and height
  They were used to rank species and understand their ecology
- Also tradeoffs along these axes and what does it mean for ecology of plants?
- Change in allometry due to change in environment

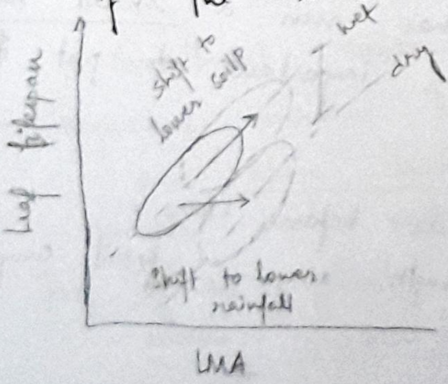
Curve is initially negative due to construction costs, and then increases

It's a saturating curve because the leaf is senescing, it not as efficient anymore



Also, as leaf gets older, it gets shaded by other leaves that are newly growing

- When should the tree drop the leaf?
  Not before A and definitely by C, so it should be between B and C. On the right hand side of B, the returns will be less as compared to if the same amount were invested in another leaf.



- Relationship b/w leaf traits and how they change with environment

Slope can change, elevation can change or just translation along same slope

(11) Diaz et al paper

- They had 4 hypotheses about how the traits are distributed
    1. Uniformly distributed & independent from each other
    2. Normally distributed & independent
    3. As observed & independent
    4. Normally distributed and not independent

This is distribution in multi dimensions.

The data best supports the 4th hypothesis.

Lecture 20/4

Ecological Impacts of Climate Change

Climate change

What can cause climate change?
- Sun's output
- Drifting continents
- Earth's orbit
- Volcanic eruptions
- Greenhouse gases

Greenhouse effect

All wavelengths of light are allowed to enter, but outgoing longwave radiation is reflected back and not allowed to escape - this warms up the greenhouse

Greenhouse gases - water, CO_2, CH_4

These gases absorb longwave radiation. Water vapour conc hasn't changed over long time, whereas CO_2 has be increasing rapidly.

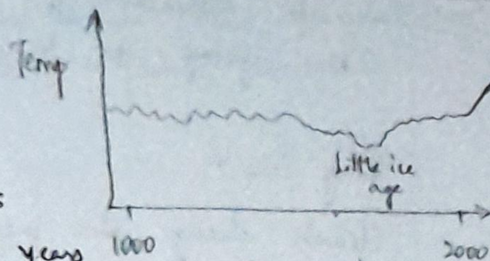
Earth's temperature globally has seen a steady rise since 1900s. But it's important to put it in long term context

How do we temperature records before 1800s?

Annual tree rings & growth rings, fossil composition and air bubbles in ice core

Reconstructed temperature records

There was medieval warm period & little ice age, but current temperature rise is unprecedented in last ~1000 years



Hockey-stick

But when we look at records of 100,000 years, we can see large changes in temperature, which varies periodically, with some stochasticity.
CO_2 levels and temperature are correlated.

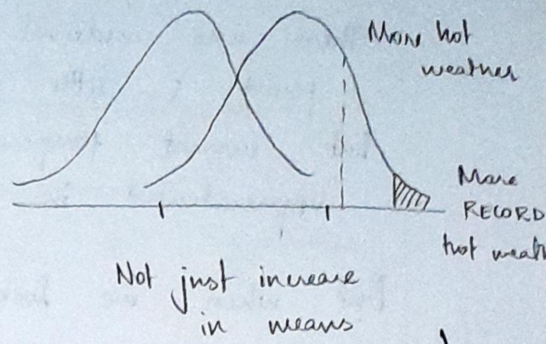
Could the current warming be natural?
The current rise in CO_2 is well above the natural limits and mainly caused by industrialization
Modelling shows that if we exclude CO_2 increase, natural forcings only would have cooled
So, climate change is mainly caused by anthropogenic activities.
Also, global warming is unequivocal.

Temperature increase scenarios
Different earth system models try to project temperatures based on different scenarios.
B1 - Business as usual -
Commitment scenario
- Temperature increase is much greater in the poles, and above landmasses as compared to the equator and water.
- Temp change globally can be 2°c, but ~~on~~ this means 7°c increase at the poles.

46

Climate change in India

Temperature predictions are not very precise, but it's going to increase. It is also predicted that rainfall is going to be higher.



Why care?

Climate change also increases the probability of more extreme climate

21/4

Lecture

Projected impacts of climate change on -

- Food availability - fall in crop yeilds
- Water : glaciers disappear, sea level rise
- Ecosystems : damage to coral reef
- Extreme weather events
- Risk of irreversible events.

2017 Conclusions

Warming is inevitable, human-caused warming over last 30 years has likely had a visible influence on physical & biological systems

Continued emissions would cause further warming, and if it goes beyond tipping point, then it would be hard to go back to prewarming temperatures.

Consensus

Do we know enough about drivers of climate change?

Are we underestimating Earth's complexity?

Can models accurately simulate complex climate system?

Are there processes that will naturally limit warming?

There are a lot of questions, but also accumulating evidence – arctic ice melting faster, emissions have also increased.
Climate scientists are mostly agree on climate change and it's causes.

What can we do?

- Increase energy efficiency, use alternate energy sources
- Develop carbon capture and storage (terrestrial, ocean sequestration)
- Better land use strategies
- Decrease deforestation

CO_2 emissions have been increasing rapidly. Top emitters are US, China, Europe, Canada & India. When it's per capita emission, US, Europe and Canada are highest

Effects of climate change on ecosystems

1. Decrease in reproductive yeilds (but not necessarily for every organism – not for eurytherms, temperate ecosystems
2. Change in phenology
3. Change in distribution – local extinctions, increase in invasive species.
4. Change in community structure and composition
5. Loss of biodiversity.

Relative effect of drivers
- Land use > Climate > N deposition > Biotic exchange > Atmos CO_2

overall global relative effect ↑

For arctic, alpine and boreal ecosystems, climate change is the major driver, but for tropical, grassland, lakes and temperate ecosystems, it is land use change

Climate and phenology

NAO and spring temperatures are closely related

Flushing of leaves and migration & hatching of two birds are also correlated,

But since 1950, over time, these systems are going out of sync

Lecture

22/4/22

Mouillot paper discussion

- Premis

There's huge loss of diversity, which leads to loss of function (BEF). Does loss of species diversity lead to same functional diversity? And does the loss of FD lead to same loss of BEF?

- What did they do?

Objectives – clear questions, what did they study

Study system

Space: global study of tropical reef fish communities.
- Species rich
- highly vulnerable to climate change
- gradient of species diversity

Objective: See how sp. div and fn. diversity are correlated

They don't measure BEF!

- What did they measure? Methods?

They measured some traits (body size, diet, mobility, vertical position, time of activity & schooling) for 6,300 species. They created combinations of these traits, called functional entities.

Through these functional entities, they wanted to understand distribution of trait combinations, functional redundancy (greater no. of species in lesser fn. entities) and functional vulnerability.

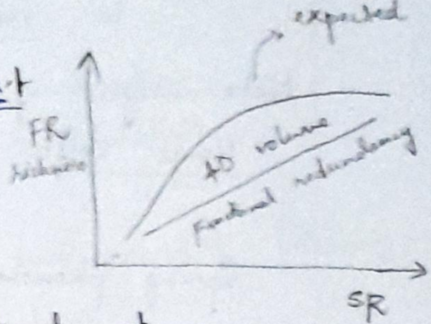
functional vulnerability – how losing a species will affect the functional entity
Functional over redundancy – how often the $\frac{S}{FE}$ value is above average for various FEs.
How FR, FV and FOR are correlated with species div?

→ Results
Relative richness of no. of species, no. of FE and 4d volume (through PCoA)

27/4/22

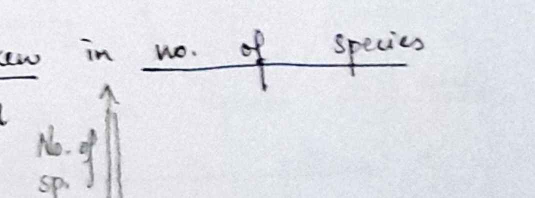
Lecture

large difference in sp. richness doesn't show a proportional difference in functional richness



But we don't see a saturating curve – it's because we are already at a very high sp richness (500), so we're not seeing the sharp increase initially.
If FR-SR relationship is linear, then there's no redundancy. But the way they calculate slope, this relation is also linear.

There's a very asymmetric skew in no. of species per functional entity in all biogeographic realms. ⇒ Many fn. entities have just one species in them.



- When trying to look at problems – compare their broad objectives to their results and inferences they make at the end

Toussaint paper discussion 28/4/22

Oops

Lecture 29/4/22

Ecological effects of climate change

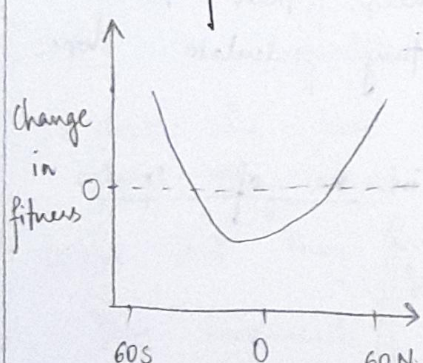
Land use change is major driver of species loss in the tropics.

Biological impacts of global warming (Walther et al 2002)
- Increased anamoly in phenology of plants & animals
- Decrease in no. of frost-free days and increase in exotic species numbers

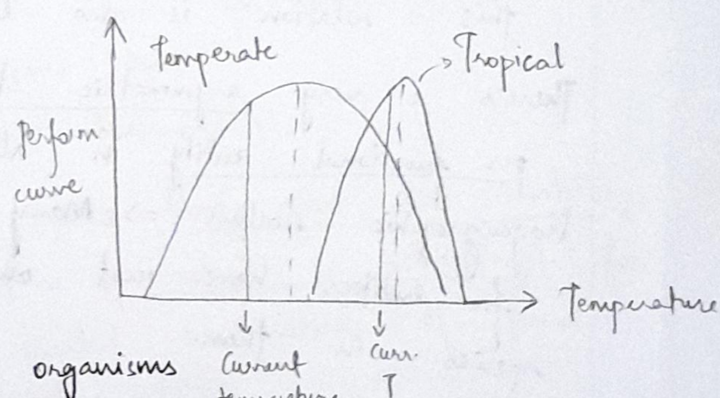
Meta-analysis of 1700 species
Range shifts - 6.1 km per decade towards pole
6 m per decade in altitude

Spring phenology

Tropical organisms may be more vulnerable to global warming
They measured the thermal performance curve for ectotherms across the latitude, and based on expected T rise, they measured the change in fitness for ectotherms



O'Sullivan 2016



This is because temperate organisms have broader niche breadth (∵ of interannual variation in T) and their current temperature is lesser than their optimal temperature, so their fitness is going to increase
Similar results have been shown for trees.

Biotic interactions and community is also going to change

Novel competitors are likely to shape species responses to global warming - Alexander et al 2015

They transplanted communities of plants across alpine elevation gradient and confirmed that biotic interactions are going to affect climate change response

Climate change affects all levels of organisation -

Genetic
Physiology
Morphology
Phenology

Population dynamics
Distribution
Interspecific interaction
performance & productivity

How do functional traits relate to environmental filtering?

Dispersal - seed traits are important

4/5

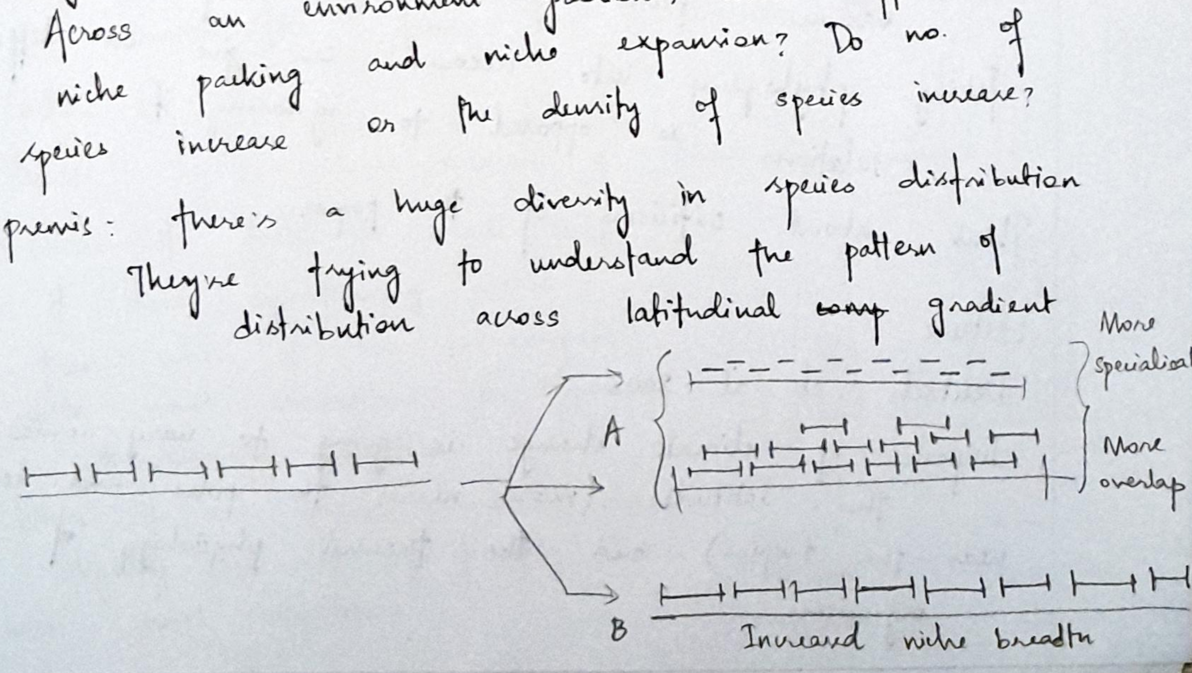
Lecture

Pigot paper

Across an environment gradient, what happens to niche packing and niche expansion? Do no. of species increase or the density of species increase?

premis: there's a huge diversity in species distribution

They're trying to understand the pattern of distribution across latitudinal ~~comp~~ gradient



(52)

They want to see if it's mechanism A or B

Specific objectives - classify based on functional groups and morphological traits
constructed a morphological niche space, and see how it changes with latitudinal gradient

Morphological traits - beak size, tarsus length, wing length and tail length

Ecological guilds - specialist insectivore, granivore, frugivore, omnivore

523 passerine birds - Andes to Amazon elevational gradient

Fig 3a - % packing vs expansion

Ecological specialisation - distance of functional trait space from the centroid of the volume

Ma et al 2021

Understanding relationship between traits and environment of bears, & try connect it also with their phylogeny

Usually, phylogeny is not considered - data points of various species are considered independent

Taking phylogeny into account can give us different relations as opposed to ignoring it.

Think about criticisms of the paper.

5/5/22

Lecture

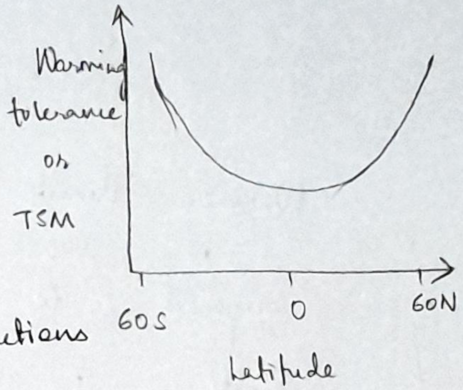
Deutsch et al 2008

Impacts of climate change is going to vary across the latitudes (more nearer the poles and lesser near the tropics) and the thermal physiology of organisms.

They wanted to see how thermal performance curves of terrestrial insects changes over the latitude

Performance / relative fitness – <u>intrinsic growth rate</u> – was plotted against <u>warming tolerance</u> ($CT_{max} - T_{Hab}$) and <u>thermal safety margins</u> ($T_{opt} - T_{Hab}$) ie ΔT before species starts to die out or performance decreases.

Not much data points near the tropics



Alexander et al 2015

Indirect effects of climate change can be through biotic interactions

Objectives – See the effect on productivity based on whether –

1) Can you track climate change?
2) Who are you competing with – current or new competitors?

They do this by transplanting focal species and communities from one elevation to another.

6/5

Lecture

Results : Fig 2 - Some measure of fitness / performance

- When it fails to track temp., it does significantly worse ~~than~~ when it has to compete with novel competitors, as opposed to current competitors.
- When it can track climate, it does slightly (but not significantly) better with novel competitors.

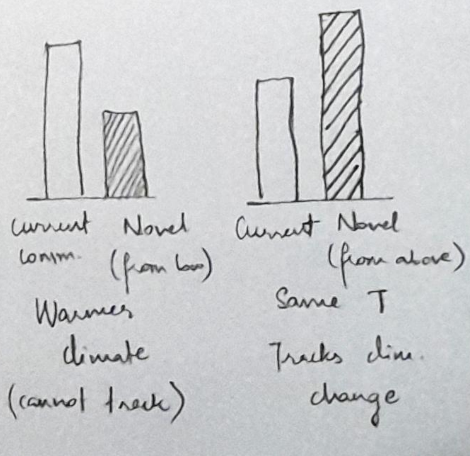
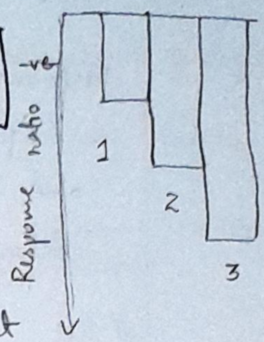


Figure 3 - Functional traits (PCA)

Plants at various elevations fall into 3 clusters, or maybe 2 (low elev - RHS ; higher elev - LHS) clusters on PCA plot.

Response ratio : $\ln \left[\dfrac{\text{Biomass with competition}}{\text{Biomass without comp.}} \right]$



1. Current climate
2. Warmer, current comp.
3. Warmer, novel comp.

Stress gradient hypothesis ; Relative neighbour effect

Warmer climate negatively affects the plants, which is worse if it has novel competitors as compared to current competitors.

Scheffers et al.

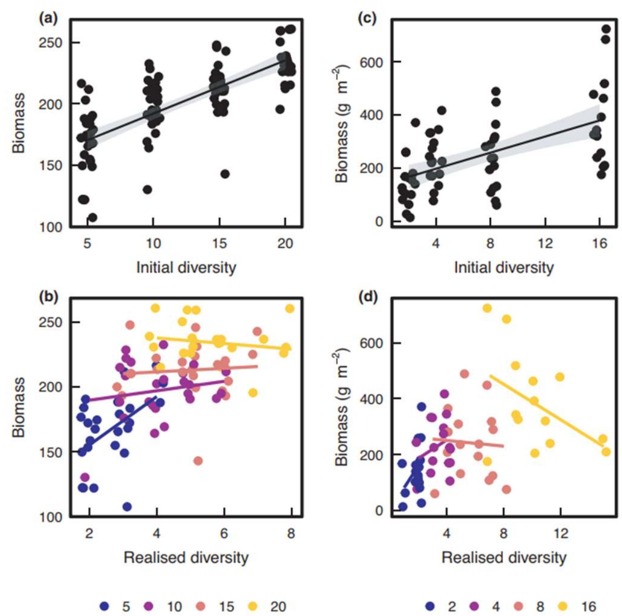
- Main results : climate change is impacting different levels of biological organisation in various ecosystems. And its going to be complicated to predict the effects of climate change on any given system - we need more <u>integrative studies</u>.
- Individual level : genetics & evolution to adapt to cc, but the timescales are different
- Physiology level : metabolism, sex determination, performance
  Responses - behavioural regulation, acclimation or migration

Hagan et al., 2021 – We shouldn't necessarily expect a positive relationship between biodiversity and ecosystem functioning in observational field data

Premise: Controlled experiments show positive relationship between biodiversity and ecosystem function (BEF), whereas observational data shows variable relations. Hagan et al. re-analyse observational datasets and argue that it's hard to interpret them, because biotic interactions filter species during community assembly. We might be seeing the effects of large biodiversity of the species pool, even while the local community composition is poor.

Summary

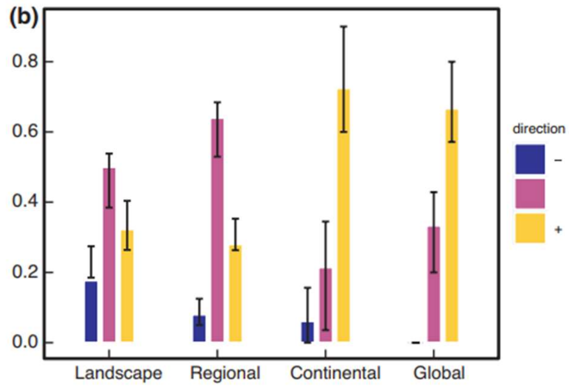
1. Introduction
    a. Experiments have shown biodiversity is important for ecosystem function, but it has been hard to identify the mechanisms (species composition, niche partitioning etc), and often they covary and feedback on each other.
    b. Consensus: BEF is a positive and saturating relationship at the local scale for a number of different taxa and habitats.
2. Applying BEF research to observational field data
    a. Local species numbers are not declining with the same ubiquity of regional/global scale species diversity. Local community composition has been changing, but no systemic decrease in species diversity at the local scale.
    b. Analysis of observational field data will tell us if local BEF experiments can be generalised to larger scales with more heterogeneity and trophic levels. Negative and unimodal BEF curves are very common results of field data analysis, possibly because they don't control for variability in environmental conditions.
3. Realised diversity should not necessarily correlate positively with ecosystem function in observational data
    a. Implicit assumption while analysing field data – number of species at present time (realised diversity) is the driver of ecosystem functioning.
    b. BEF experiments manipulate initial species diversity and this can influence ecosystem function through two methods –
        i. Complementarity effects: when CE are high, many species can co-exist and contribute to ecosystem function by portioning resources locally or through time i.e., niche partitioning
        ii. Selection effects: Portfolio effect i.e., having initial high diversity increases the chance of including the 'most productive species' in the community pool/realised density. When SE is strong, the most productive species outcompete other species and become very abundant.
    c. Through these effects, high initial diversity can increase ecosystem function when realised diversity is low or high. But in both cases, initial high diversity is very important i.e., initial biodiversity and ecosystem function has a positive relationship and this has been established by BEF metanalyses. But the relationship between realised biodiversity and ecosystem function can be positive, neutral or negative, as shown by a model (2a) re-analysis of several studies (Jena experiment (2b) and BIODEPTH)



d. Field data can show positive BEF when complementary effects are high, which means realised diversity is directly correlated to initial diversity.
e. If only realised diversity data is available, positive effects of initial diversity may not be observed.
f. Several models also predict positive realised BEF only for certain range of parameters. So, we shouldn't expect to see positive relation from field data.

4. The Local Species Pool Concept – an analogue of initial species diversity for field data
    a. Local species pool of a habitat patch can be defined as the subset of the regional species pool that can (1) tolerate the local conditions, and (2) be expected to disperse into the habitat patch over ecologically relevant timescales
    b. Local species pool can be a proxy for Initial diversity, and can help us link BEF theory to field data.
    c. Initial diversity and local species pool are not independent. In experiments, they are strongly correlated, but empirically, their relation can be quite variable. A meta-analysis found that 30% studies show no relation between initial diversity and local species pool.
    d. Realised diversity correlates strongly with local species pool diversity when –
        i. Patches have large enough spatial extent that there is variation between patches in their local species pool
        ii. processes like disturbance which enhance the colonisation success of dispersing species have been shown to make realised diversity more similar to local species pool diversity
        iii. Factors that promote species coexistence (like heterogeneity and spatial grain) increase correlation and makes BEF relation positive
    e. Given that we don't know local species pool or its relation with realised diversity in field studies, and that local species pool might not be variable among patches, we don't get to see a clear positive BEF relationship from observational field studies.
    f. They reanalysed a meta-analysis paper and saw that proportion of positive, negative and neutral studies varied with the scale of the study.

g. Doubt – does this mean effects of diversity doesn't show at landscape level, or that diversity does not impact ecosystem function at landscape level as much?



5. Correlating realised diversity with ecosystem function might underestimate the importance of biodiversity
    a. BEF theory does NOT predict realised diversity to correlate positively with ecosystem function, so no surprise when it doesn't.
    b. Even though there is no decline in local species diversity, biodiversity loss at regional level prevents local ecosystems from receiving a diverse set of colonists, which in turn affects ecosystem function.
6. Applying BEF theory to field data: Future directions
    a. To test BEF theory using field data, plot ecosystem function against local species pool, not realised diversity
    b. If we want to predict how anthropogenic change will affect ecosystem functioning, we need to understand how different pathways of change in species diversity and composition affect ecosystem functioning in response to different drivers
    c. Islands are a good model system (with limited, well-defined local species pool) on which to test BEF through observational data.
    d. Estimate local species pool of patches where observational data has been collected.
    e. In order to understand the effects of anthropogenic change –
        i. First characterize how species diversity and composition are changing in local communities through time
        ii. Then we need to understand how the observed changes will affect ecosystem function in specific taxa and habitats
7. BEF relationship with realised diversity is determined by the environment, species traits and species interactions at a variety of scales.

Westoby et al., 2002 – Plant ecological strategies: Some leading dimensions of Variation between Species

Barua said – "This review summarizes work that formed the basis for a lot of plant trait-based ecology that followed. Keep in mind that this was 20 years ago! Focus on the leaf traits and leaf economic theory parts. These form a good introduction for the next paper on the leaf economic spectrum. Understand the seed mass-seed output trade-offs sections, and the importance of plant height."

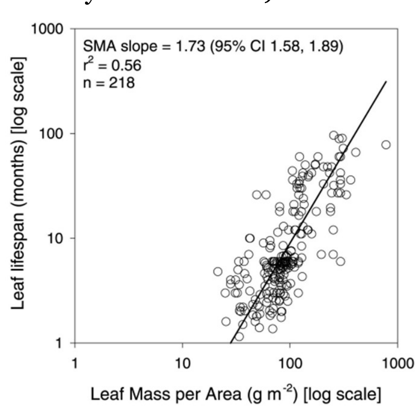
Outline of the paper: Looong Introduction; Leaf mass per area-Leaf lifespan trade-off; Leaf size-Twig size spectrum; Seed mass-Seed output; Potential Canopy Height; Conclusions and outlook. [I have only focused on the underlined sections]

Introduction

1. This review discusses four major dimensions of variation across vascular land plant species. The dimensions affect ecological strategy, that is, the manner in which species secure carbon profit during vegetative growth and ensure gene transmission into the future.
2. Several ecological strategies have been defined before. One of the major ones that didn't work out so well was the CSR (competitors, stress-tolerators, ruderals) strategy, which focuses on ability to cope with stresses, and adapt to slow vs fast growth rates.
3. Criteria for ranking a dimension of variation – ecological significance, spread and consistency, practicality for literature synthesis (easily quantifiable)
4. Types of correlations between traits –
    a. Physical trade-offs – seed mass and number, leaf lifespan and mass per area
    b. Favoured by available niches – Habitats with tall stem might also select for larger seed mass. Looser correlation than physical trade-off
    c. Evolutionary divergence of traits – certain trait combinations persist in a lineage

Leaf Mass per Area (LMA) and Leaf Lifespan (LL)

1. Species with longer Leaf lifespan have higher LMA, which means they have thicker laminas, protruding veins, and higher tissue density – structural strength which is important for longevity.
2. Higher LMA protects against wear and tear and also deters herbivory. Species with lower leaf turnover should spend more of defence against herbivory. (What if they have lower turnover because they're defensive?)



3. Leaf economics and theory of leaf lifespan

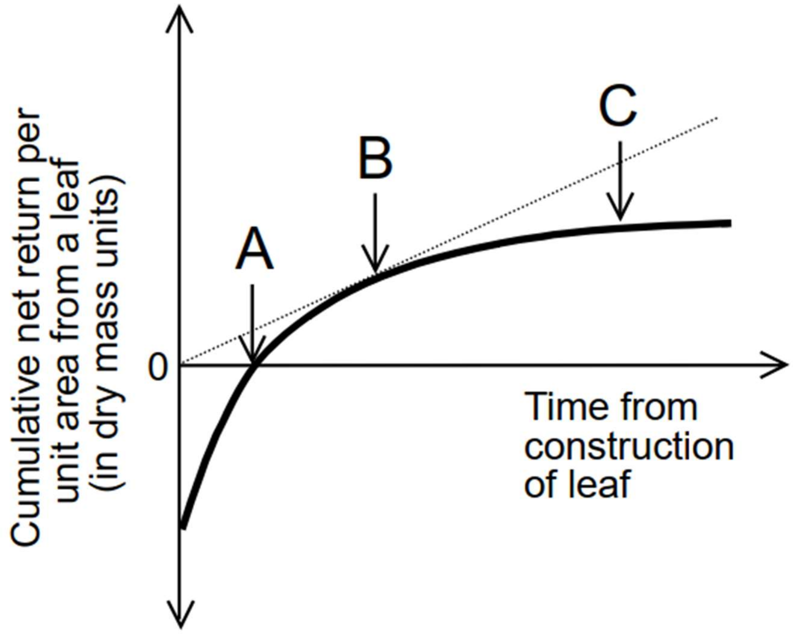


Figure 2 Essentials of existing theory for leaf lifespan (Kikuzawa 1995). Curve shows cumulative dry-mass return from a unit leaf area, net of costs of leaf respiration and of root and stem activity to support the leaf's photosynthesis. Curve is initially negative owing to construction costs (leaf mass per area), then increases through a leaf's lifetime. Payback time for the investment is at A. Net dry-mass return per time per leaf area is the slope of a line from the origin to the curve. It is maximized at the lifespan B. This optimum at B, and also payback time A, shift to longer lifespan if the cumulative dry-mass gain curve is shallower (slow-revenue environments) or if the initial investment is greater (higher leaf mass per area). At C, approximately, the leaf is no longer returning net dry-mass revenue.

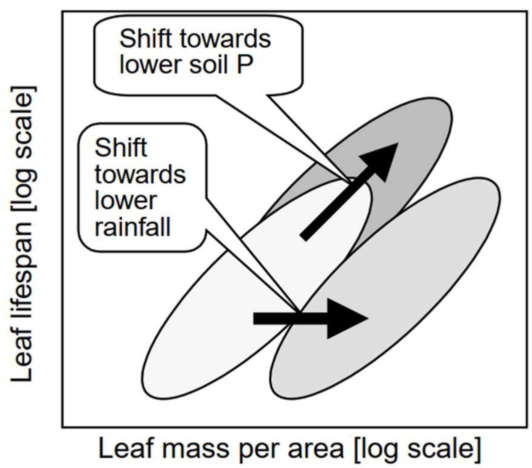
4. Replacing an old leaf with a new leaf becomes justified when the current return on an old leaf falls below the expected rate of return averaged over the life of a new leaf (point B).
5. In species with higher LMA the curve starts more negative, and similarly points A and B are both shifted to longer lifespan.
6. Leaves with lower LMA have –
    a. Higher photosynthetic capacity per unit mass
    b. Higher leaf Nitrogen concentrations (reflects the conc of rubisco etc)
    c. Shorter diffusion path from stomata to chloroplasts
7. The variation of LMA and LL is 3 to 50-fold in coexisting plants. Why do we see such a wide variation?
8. Advantages of low LMA - high photosynthetic capacity, and generally faster turnover of plant parts permit flexible response to the spatial patchiness of light and soil resources, giving short-term advantages over high-LMA species.
9. High LMA-LL species have longer-term advantages. Longer mean residence time of nutrients permits a progressively greater share of nitrogen pools in a habitat to be sequestered; slow leaf litter prevents fast growing competitors to colonise the area.

These species tend to accumulate greater total leaf mass and larger overall leaf area, so their productivity is similar to or higher than low LMA plants.

10. The slope of LL and LMA is steeper than 1 i.e., more increase in lifespan for one unit of LMA. Why isn't there a selection towards high LMA only? – leaves have to be shed at some time, high LMA trees get shaded by their canopy leaves, there is also herbivory and other wear and tear, which is more costly for high LMA.

LMA-LL Trade-off in different environments

1. High LMA is a cost to the plant. Long LL requires high LMA because of the physical constraints, the leaf has to be engineered to withstand wear and tear, which is only possible by increasing LMA.
2. LMA required for some LL would depend on two factors –
   a. the wear and tear on a leaf might be more severe in some environments than others.
   b. leaf tissue might be softer in some environments than others, such that a greater lamina depth is required to achieve a given overall structural strength. Low precipitation requires more LMA to increase LL as compared to high precipitation area.
3. Shaded understory species (low wind, high humidity, low risk of wilting) have longer LL at lower LMA as compared to well-lit species. The same is true for sun leaves and shade leaves. So, it's not one LMA-LL relationship, rather based on the environment, the curve can shift



Conclusion

These three dimensions of variation capture important generalities about how plant species make a living. They can be measured relatively easily, which is important if they are to serve for coordinating information worldwide.

Toussaint et al., 2016 – Global functional diversity of freshwater fish is concentrated in the Neotropics while functional vulnerability is widespread

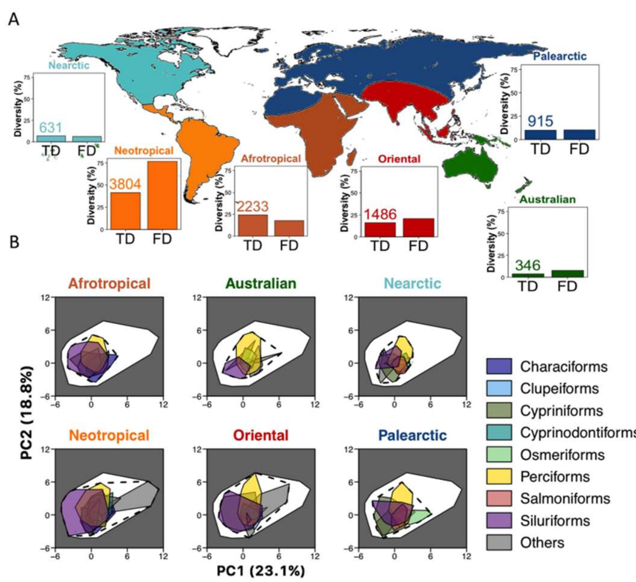
Premise: Biodiversity measurements usually only focus on taxonomic component of biodiversity and not functional diversity (which is a measure of the range of functions carried out by organisms).

Methods:

1. They assess 10 morphological traits (proxy for functional traits of food acquisition and locomotion) of 9,170 species across 6 biogeographic ranges.
2. Functional diversity (FD) is calculated as the volume filled by the species in a multidimensional space defined by morphological traits.
3. Functional uniqueness of each order of fish (F_{uniq}) is defined as the proportional of functional space that is only occupied by that order.
4. Functional vulnerability (F_{vul}) is defined as the proportion of space occupied by species that are on IUCN's threatened or endangered list and endemic species that occupy single river basin.

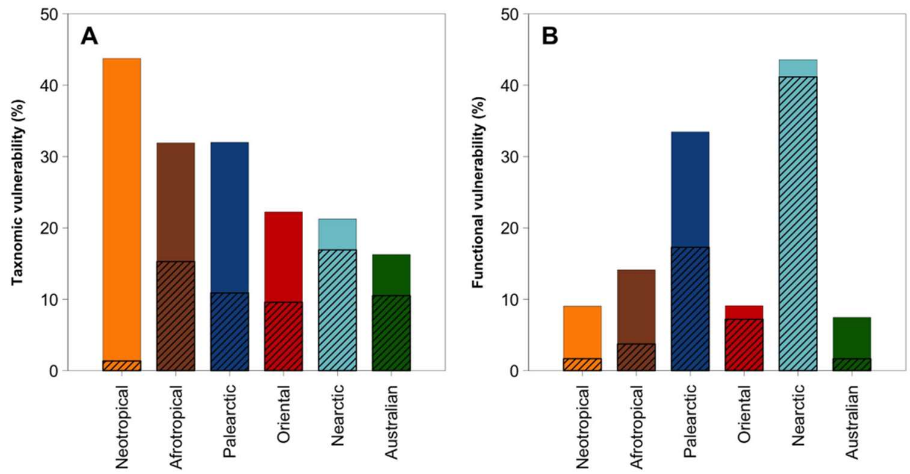
Results:

1. Neotropics host more than 75% of world fish FD



   a. There is a shared functional core across all realms.
   b. Noetropics have 75%+ FD, and the next highest realms have about 17-20% each. Neotropics taxonomic diversity (TD) is 2x, whereas FD is 4x.
   c. Neotropical fauna has a significantly larger FD than expected from its TD, while the same is not true for other realms
2. Differences in FDs are driven by F_{uniq} of a few fish taxa
   a. Neotropics has more uniquely shaped fish than other realms, especially because of one order (Siluriforms)
3. Functional vulnerability is highest in Palearctic and Nearctic 'despite' (maybe it should be 'because') of their low functional diversity [Figure 4]
   a. Neotropics face the largest taxonomic vulnerability, but low functional vulnerability probably because of the functional redundancy

b. Conservation efforts should focus more on Palearctic and Nearctic



Critique

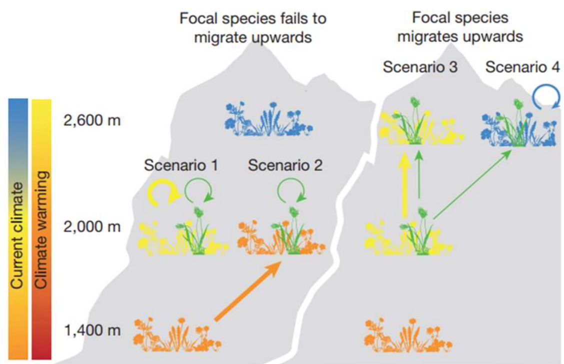
Could have also measured functional redundancy (from Mouillot et al.) to see if it is correlated to functional vulnerability.

Alexander et al., 2015 – Novel Competitors shape Species' Response to Climate change

Premise: The direct effects of climate change on physiology and demographics have been well studied and established. The paper tries to study the indirect effects of climate change – by studying its effects on community composition and in turn, how it would affect biotic interactions of a species.

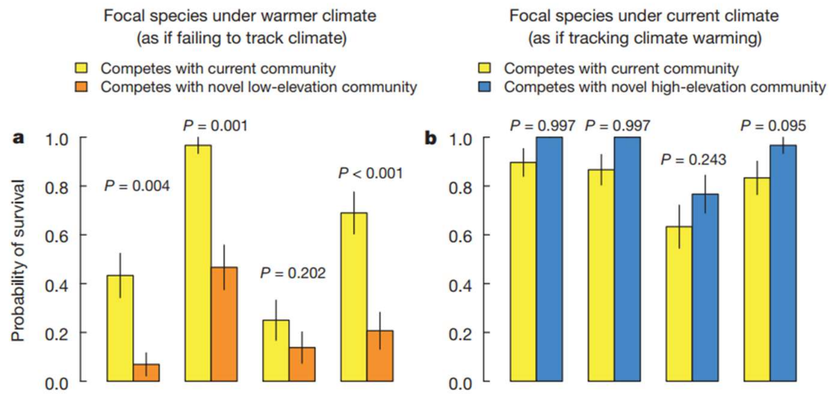
Methods: Transplant communities across elevation gradients in Swiss Alps – 1,400m, 2,000m and 2,600m.

1. The focal species could fail to track climate change such that its temperature would increase in the future. In which case, it's neighbours could be a) its current competitors or b) novel competitors from lower elevation that have tracked the temperature. If the species manages to track climate change and migrate up the elevation gradient, then its competitors could still be – c) its current competitors that have tracked climate along the focal species or d) novel competitors from higher elevation that have failed to track the temperature. [Figure 1]
2. While transplanting communities, they controlled for soil composition, herbivory rates, soil biota, and confirmed that novel competitors were the main reason for the difference in biomass observed.
3. They also measured functional traits of 61 species

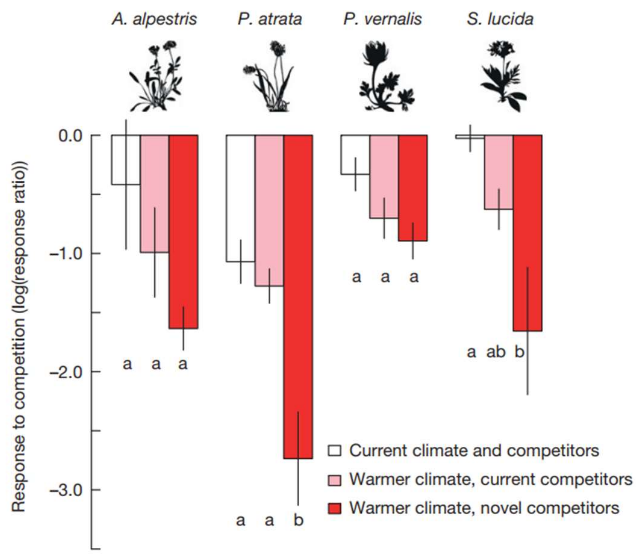


Results

When the species fails to track climate change, it does significantly worse when it has to compete with novel competitors (from lower elevation) as compared to its current competitors. When it tracks climate change and moves up the elevation gradient, the competitors (current vs novel) don't have a significant effect on probability of survival, biomass or probability of flowering [Figure 2a, 2b, 2c].



Similar results are shown by ln(response ratio) where response ratio = biomass with competitors/biomass without competitors. [Figure 4]



Through PCA analysis of 5 functional traits, they found that low elevation plants are functionally dissimilar to mid- and high-elevation plants, which are similar to each other. So, competition becomes an factor when the focal species cannot track climate change.

Critique

Overall nice paper, good controls. They dug up plots of land and transplanted it across altitude using helicopters => hard to replicate the results in an experimental study. Can't think of anything more; let me know if you do.