Insect Declines Essay Plan

*Insect groups and uses:*

Sanchez-Bayo, 2019 – Lepidoptera: pollination, natural pest control, prey items. Hymenoptera: bees for pollination and economic value. Diptera: pollinators, natural enemies of agricultural pests. Coleoptera: largest order of insects, pest control and recycling of organic matter. Hemiptera: true bugs. Orthoptera: grasshoppers, locusts, crickets. Odonata: dragonflies and damselflies. Predators of aquatic and flying insects. Control mosquitos and agricultural pests.

Powney, 2019 - ecosystem health and for global food security

Cardoso, 2020 – lose species, abundance, biomass, diversity, parts of tree of life (insects are most successful taxonomic group on the planet and therefore constitute a major branch of the tree of life), unique ecological functions and traits (i.e. functional diversity), fundamental parts of networks of biotic interactions. Get homogenization, simplified networks.

Habel, 2019 – pollination has high economic value, and significant impact on crop yields.

Montgomery, 2020 – recent reports are sufficiently robust to justify immediate action.

*Drivers:*

Sanchez-Bayo, 2019 - A large proportion of studies (49.7%) point to habitat change as the main driver of insect declines. Includes urbanization, agriculture, industrialization. Land use change and landscape fragmentation. Pollution (fertilizers/pesticides), biological factors (parasites/pathogens/invasive species – direct or indirect), and climate change (worse for tropical regions as have narrow thermal thresholds) also drivers.

Powney, 2019 - Key threats to pollinators include agricultural intensification (particularly habitat loss and pesticide use), climate change and the spread of alien species

Habel, 2019 – review. Agricultural intensification is the main driver of recent terrestrial insect decline. Supplementary and adversely synergistic factors especially climate change, urbanization, and pollution. Habitat loss, isolation, and decreasing quality reduce gene flow and alter meta-population structure. Fertilizers often lead to flowering herbs being replaced by grasses. Climate change – range shifts, extreme weather events.

Lister and Garcia, 2018 – climate warming. BUT increased exposure to extreme temperatures may have a greater impact on fitness than gradual increases in average temperatures.

Soroye, 2020 – climate change increases frequency of environmental conditions that exceed species' tolerance. Marginal areas could become more suitable, making colonization of that locale more likely. Can have direct effects on mortality and fecundity, and indirect effects through changes to floral resource.

Deutsch, 2008 – warming most likely to have most deleterious consequences on tropical insects which are sensitive to temp change, and currently living very close to their optimal temperature. Intrinsic rates of pop growth expected to decrease by up to 20%, thereby lowering fitness. Warming tolerance of tropical insects is only 1/5th that of mid-latitude insects. Concern as greatest risk of CC is in the tropics where BD is greatest. Higher latitude species have broader thermal tolerance, warming may even enhance their fitness.

Outhwaite, 2022 – interaction between land-use change and climate change. Use PREDICTS. Data span 20 years (1992-2012) but individual studies often only collected data over very short time span. Warming equivalent to 1 s.d. of baseline temperature variation led to 49% and 27% reductions in insect abundance and species richness in intensive agriculture, respectively, compared with those in primary vegetation with no climate warming. Under the same level of climate warming, low-intensity agriculture experienced 30% and 23% reductions in insect abundance and species richness, respectively. Biodiversity in lower-intensity agricultural systems is partially buffered against the negative impacts of increases in extreme temperature.

Cardoso, 2020 – often several factors contributing synergistically. Habitat loss and fragmentation: deforestation, agricultural expansion, urbanization, decreased connectivity = range shifts are constrained. Pollution: fertilizers, industrial, light. Invasive species (direct or indirect effects). Climate change, overexploitation (unsustainable harvest for pets or decoration), food, medicine. Co-extinction.

Van Engelsdorp, 2009 – CCD – rapid loss of adult worker honeybee, no single measure emerged as most likely cause. Spatial autocorrelation suggest CCD is either a contagious condition or results from exposure to a common risk factor. pathogens seem likely to play a critical (albeit secondary) role.

Dicks, 2021 - global-scale expert assessment of drivers and risks associated with pollinator decline. Risks higher in global south, where there is high diversity of insect-pollinated crops grown and high diversity of extant indigenous cultures and people, but evidence mostly concentrated in high-income countries, which had lowest risk. Subjective due to personal opinions?

*Study findings:*

Hallmann, 2017 – insect biomass, Malaise traps, 27 years (1989-2016), 63 nature protection areas, Germany. Seasonal decline of 76%, regardless of habitat type, while changes in weather, land use, and habitat characteristics cannot explain this overall decline. Not only vulnerable species. Temporal changes in climatic variables changed in a manner that should have increased insect biomass (e.g temperature). Could not incorporate agricultural intensification. Almost all locations (94%) enclosed by agricultural fields.

Sanchez-Bayo, 2019 – review of 73 historical reports of insect declines, "global" (but mostly Europe and N America). Dramatic rates of decline that may lead to the extinction of 40% of the world's insect species over the next few decades. Common/generalist species, as well as specialists. Abundance of small number of species is increasing (adaptable/generalists). Estimate the current proportion of insect species in decline (41%) to be twice as high as that of vertebrates.

Simmons, 2019 – response to Sanchez-Bayo, 2019. Biased towards studies which report declines, geographic bias, threats are postulated (not statistically tested), polling papers is not the same as synthesizing quantitative evidence.

Powney, 2019 - substantial inter-specific variation in pollinator trends, based on occupancy models for 353 wild bee and hoverfly species in Great Britain between 1980 and 2013. Losses concentrated in rare species. Losses linked to specific habitats – 55% decrease species associated with uplands. 12% increase in dominant crop pollinators. Third of wild pollinator species (33%) have decreased over this period, approximately a tenth have increased, with the remaining species showing no clear trend. Similar overall declines for bees (25%) and hoverflies (24%) but all severe bee decline occurred post 2007, whereas hoverflies declined steadily from 1987 to 2012. Eusocial bee species average occupancy increased by 38%, solitary bees decreased by 32%.

Outhwaite, 2020 – Terrestrial insects (also looked at bryophytes and lichens) increased in average occupancy. More complex pattern of BD change in UK than previously reported. Over 5000 species, 11% higher occupancy in 2015 compared to 1970, though substantial difference between groups. Rare species showed greater change.

Biesmeijer, 2006 – bee and hoverfly, UK and Netherlands. Rarefaction methods to compare species richness. Evidence of declines in bee diversity in both countries, but divergent trends observed for hoverflies. Declines more frequent in habitat/food specialists, univoltine species, and/or nonmigrants. Plant species reliant on declining pollinators then also declined. Signif decreases in richness observed in 52% and 67% of British and Dutch cells. Increases in 10 and 4%. No signif directional change for hoverfly richness in UK, but increases in 34% and decreases in 17% of Dutch cells. No direct measurement of population densities. Increase in domination of pollinator communities of both countries by smaller number of species. Shifts in pollinator traits suggest possible shifts in pollination services.

Ollerton, 2014 – historical records, assessed rate of extinction of bee and flower-visiting wasps, Britain, mid 19th century – present. Most rapid phase of extinction from 1920-50s with changes in agricultural policy/practise./intensification. 3.41-3.46 species per decade. Slowing of extinction rate from 1960s – 0.98 species per decade. Due to prior loss of most sensitive species? Or effective conservation programs? Correlational reasoning.

Hallmann, 2020 – beetles, moths, caddisflies, Netherlands, 1997-2017, annual rates of decline of 3.8, 5.0 and 9.2%, respectively. Declines of ground beetles (Carabidae) stronger after 1995. Abundance measure: Macro-moths – trends of individual species comparable to overall trend BUT ground beetles – abundant performed worse than rare. However, for biomass measure of ground beetles, rarer species showed stronger declines. Suggests biomass may not always show one-to-one correspondence to numerical declines. When translated into biomass estimates, our calculations suggest a reduction in total biomass of approximately 61% for macro-moths as a group and at least 42% for ground beetles, by extrapolation over a period of 27 years. Compare to 76% reduction that Hallman, 2017 found for flying insect biomass in Germany.

Lister and Garcia, 2018 – 1976-2012, Puerto Rico rainforest where temps have risen by 2 degrees. Dry weight biomass. Sustained declines (across all 10 of the major taxa captured) over the 2 decades. Climate warming is the major driver due to average ambient temp being signif predictor in abundance. Also, signif human perturbations have been virtually non-existent. BUT shifts in distributions could have caused patterns? Some argue land use change causes warming, but unlikely to be the case here.

Seibold, 2019 – looked at arthropod occurrence across gradients of land-use intensity. Data on > 1 million arthopods, 2700 species, 2008-2017, 150 grassland, 140 forest sites, 3 regions of Germany. Total number of species and overall gamma diversity decreased over time. Grasslands - biomass, abundance and number of species declined by 67%, 78% and 34%, respectively. Mainly affected rare species. Magnitude was independent of local land-use intensity, but sites embedded in landscapes with a higher cover of agricultural land showed a stronger temporal decline. Forest - biomass and species number—but not abundance—decreased by 41% and 36%, respectively. Abundant and rare species affected. Some originally abundant species actually increased in abundance.

Gillespie, 2020 – terrestrial arthropod abundance and diversity, North Atlantic region of the Arctic. >10 years, signif declines in 7/14 muscid fly species 1996-2014. Iceland moth monitoring since 1995 shows significant positive trends in species richness at two locations, but negative or non-significant trends in abundance. 1996-2016 – signif declines in total abundance of potential vertebrate prey. BUT unable to report on vast majority of groups.

Homburg, 2019 – carabid species declines in nature reserve in Northern Germany. Woodlands, 24 years, trapping study, assessed biomass, species richness, functional diversity and phylogenetic diversity. Did not observe a decline in number of individuals (abundance) or biomass, but in species richness, functional diversity and phylogenetic diversity in carabids. Smaller species showed stronger declines so diversity less represented by decreasing number of small species, maybe explaining why no decline in biomass? Assume the detected trends to be the result of external effects such as climate change and the application of pesticides BUT cannot disentangle which factor is responsible. Biomass calculated by multiplying mean body length by number of individuals – is this accurate enough?

Brooks, 2012 – carabids, UK, 15 years, 1994-2008, substantial overall declines, ¾ species studied declines. Differences between regions and habitats – 48.4% declines in northern moorland and western pasture, to 50% increases in southern downland. More stable in woodland and southern hedgerow. BUT even when stable in these sites, same taxa were often declining elsewhere. Declines often more pronounced for species adapted to very dry or wet conditions.

Fox, 2019 - 54 butterfly and 431 macro-moth species - varying the start year of the 10-year population trend had a substantial effect on whether particular species met Red List thresholds and on the overall number of species assessed as threatened.

Loboda, 2018 – high arctic fly, 2 decades (1996-2014), diversity and abundance and composition, Greenland, 18385 individuals, 16 species of muscid flies. Significant decrease of 80% of total muscid abundance. The number of common/abundant species also decreased significantly. Shift in composition in each habitat was associated with summer temp, which increased significantly over the study period. BUT no change in habitat similarity suggests no biotic homogenization across habitats. Results suggest change in species composition mainly attributable to decrease in species abundance. At species level, most relationships between abundance and climate predictors were not signif.

Boyes, 2019 – reported on winners among British moths. 51 successful species, 1968-1016, 4.5 million occurrence records. BUT in the data they used, there were still more losers than winners – of the 330 macro-moths that had published trends for both abundance and occupancy, 48 showed signif increases in both measures. Majority of winners are broadly habitat generalists. Results could be relatively localized – can't generalize. Also, success may be transient state.

Van Strien, 2019 – century of data, 80% decline, butterflies, Netherlands, 1890-2017. Grassland, woodland, heathland. Strong decline in all 3 habitats. Stabilized over recent decades in grassland and woodland, but decline continues in heathland.

Van Klink, 2020 – meta-analysis, 41 countries, 166 long-term surveys, 1925-2018. Considerable variation in trends even among adjacent sites but an average decline of terrestrial insect abundance by ~9% per decade and an increase of freshwater insect abundance by ~11% per decade. Patterns were largely driven by strong trends in North America and some European regions. Freshwater increases may partially counter negative terrestrial BUT freshwater only represents ~2.4% of earth's terrestrial surface so even though the combined model for both freshwater and terrestrial showed no directional trend, the model is likely to be a poor representation at any spatial scale. No evidence for any associations between insect trends and climate change at local or region scale. Data was not representatively spread across the world – protected areas were over-represented so locations where human land use is most intensive, and thus where the strongest effects on insect trends might be expected, were underrepresented.

Wepprich, 2019 – butterfly, abundance, 20 years (1996-2016), Ohio. Total abundance is declining at 2% per year, resulting in a cumulative 33% reduction in butterfly abundance. Three times as many species have negative population trends compared to positive trends. Even common and invasive species are declining. Trends distributed across the phylogenetic tree. Univoltine species had more negative pop trends.

Soroye, 2020 – climate change, bumble bees, across continents. 66 species, North America and Europe. Increasing frequency of hotter temperatures predicts species’ local extinction risk, chances of colonizing a new area, and changing species richness. Effects are independent of changing land uses. Probability of site occupancy declined on average by 46% (±3.3% SE) in North America and 17% (±4.9% SE) in Europe relative to the baseline period. Declines more likely in sites that became drier. Rates of climate change–related extirpation among species greatly exceed those of colonization.

De Palma, 2015 – PREDICTS synthetic analysis. 257 bee species, 1584 european sites. Models where interactions were excluded (additive models) explained 13% and 37% less variation in occurrence and abundance, respectively, than the interactive models did. The effects of ecological traits on species’ sensitivity were not always consistent across land uses. Shorter flight seasons – the most important trait in explaining occurrence and abundance patterns – maybe because this trait confers a higher risk of asynchrony with key floral resources? Our data set is large, but only contains 12.5% of European bee species, with biases towards Western Europe and bumblebees.

Gray, 2016 – PREDICTS synthetic analysis – collated primary data (not effect size). Globally, species richness is 10.6% higher and abundance 14.5% higher in samples taken inside protected areas compared with samples taken outside. Mostly attributable to differences in land use between protected and unprotected sites. Analysing only the sites within each study for which land use could be matched across the protected area boundary, we found no significant effect of protection on any biodiversity measure for any management category group, taxonomic group or latitudinal zone. Protected areas are most effective where they minimize human-dominated land use.

Newbold, 2014 – PREDICTS synthetic analysis. Inverts, herptiles, mammals, and birds. Not all species respond equally to land-use change. Large, slower-breeding, less-mobile species that are dietary and habitat specialists are typically more vulnerable to land-use change than other species. Looked at major land-use type, forest cover, removal of vegetation in the 3 years prior to sampling and human population density. The probability that species occurred at a site was strongly related to the major land-use type (declined in human-modified habitat), and this response differed markedly among taxonomic groups. Increased dominance by smaller numbers of taxa. Most variation remained unexplained.

Newbold, 2016b – uses PREDICTS (not just inverts). Strong impact of land use on assemblage composition. Effect weaker in temperate compared to tropical.

Newbold, 2016a – PREDICTS, most of the world’s land surface is biotically compromised in terms of BII (Biodiversity Intactness Index) and within-sample richness of originally present species.

Millard, 2021 – PREDICTS and new database, land-use type and intensity, 4502 pollinating species. Increasing land-use intensity from minimal to intense use was associated with a significant change in pollinator biodiversity. Biodiversity was often higher at low intensity. Effects of land-use intensity were strongest in urban areas. Divergent effects between non-tropical and tropical zones. Non-tropical – richness and abundance did not differ significantly among cropland intensity classes. Higher in minimal-intensity cropland than primary vegetation. BUT tropical – richness and abundance decreased between primary vegetation and high intensity cropland.

*Lots of variation*

Wagner, 2021b - much variation—across time, space, and taxonomic lineage

Outhwaite, 2020 - enormous variation among taxa in the temporal patterns of change and the relative fates of rare and common species.

Cardoso, 2020 – specific trend and strength is not universal and changes according to taxon and region. Numerical declines of common and widespread species impact the functioning of ecosystems more severely. Threatened species tend to share biological traits that influence their extinction risk. In general, specialists in either habitat type or feeding regime, very small or very large species, and poor dispersers, are at highest risk.

Habel, 2019 – above-ground terrestrial, soil insects, and freshwater insects face different, but sometimes overlapping stressors. BUT all 3 affected by climate change. Any one driver at one time depends on the specific driver at a particular time.

Brooks, 2012 study – even when taxa stable in one environment, declining in another.

Boyes, 2019 – responses of moth winners are heterogenous, suggesting multiple drivers.

Wagner, 2021a – moth biodiversity trends are complex and heterogenous. Rates of decline for dietary and ecological specialists are steeper than those for ecologically generalized taxa. Moth trends vary at continental, regional, and even local scale. Considerable within-country heterogeneity. Drivers may interact additively, synergistically, or antagonistically and operate at different locations and over different time periods.

Hudson, 2017 - Average responses of species to human impacts typically vary among higher taxa and ecological guilds.

De Palma, 2015 - pressures are unlikely to affect all species identically, but are expected to be mediated by species’ traits e.g. social species may be more sensitive in intensively used cropland – where enhanced foraging capacity can increase exposure to pesticides and thus affect mortality and colony success – but relatively less sensitive in urban areas, where greater foraging capacities may enable persistence.

Habel, 2019 – underlying assumption at drivers act as filters allowing certain species to survive. Rapidly developing and mobile taxa less affected.

Dirzo, 2014 – "sixth extinction wave" extends across taxonomic groups, but some taxonomic groups and regions are particularly affected. Extinction risk is often a synergistic function of both intrinsic species traits and the nature of threat.

*But not all insects are declining:*

Wagner, 2021b - Not all insects are declining

Boyes, 2019 – biodiversity trends are not universally negative.

Wagner, 2021a – moths – even in studies showing clear overall declines, some fraction is increasing. Unaware of any instance where all lineages are in collapse.

Saunders, 2020 - All of the studies showed increases or no changes for some of the focal taxa across the analyzed time period.

Crossley, 2020 - No net insect abundance and diversity declines across US Long Term Ecological Research sites. >5,300 time series, 4-36 years, 68 natural and managed areas. Some decreased (32%), some unchanged (43%), some increased (24%). Lack of trend consistent across feeding groups, and similar for heavily disturbed vs relatively natural sites, and between aquatic vs terrestrial. No variables could reliably predict direction or magnitude of abundance trends. BUT Welti, 2021 says they used unsuitable datasets and did not take sampling effort into account.

*Gaps in knowledge/issues:*

Hallmann, 2017 - number of studies on insect trends with sufficient replication and spatial coverage are limited and restricted to certain well-studied taxa.

Hallmann, 2017 - To what extent total insect biomass has declined, and the relative contribution of each proposed factor to the decline, remain unresolved. urgent need to uncover the causes of this decline, and its geographical extent.

Wagner, 2021b – too little data to compare how steep insect declines reported for Western Europe and California compare to pop trends in sparsely populated regions and wildlands. Long-term species-level demographic data are meager from the tropics, where considerably more than half of the world’s insect species occur. Long-term monitoring data often come from locations that have remained largely intact for the duration of the study.

Wagner, 2021b - Considerable uncertainty remains about the relative importance of these stressors, their interactions, and the temporal and spatial variations in their intensity. Essential time-series data on the rates, geographic scope, ecological aspects, and taxonomic nature of insect population trends are scant, relative to those for vertebrates.

Wagner, 2021b - It is particularly urgent to know to what degree climate change is driving losses in the tropics, in mountains, and other wildlands away from pronounced anthropogenic activity.

Wagner, 2021b - there exist many datasets that remain unanalyzed.

Sanchez-Bayo, 2019 – apart from bees, status of most other hymenopterans e.g. ants remains practically unknown

Powney, 2019 - Large-scale evidence on species-specific trends among wild pollinators are lacking. Published data on species-specific trends are currently only available from field-scale experiments typically spanning short time periods(<5 years) and spatially restricted to a limited number of sites. Data collected via volunteer recorders lack standardized protocol/sampling bias. Also temporal bias, with more records in recent years.

Outhwaite, 2020 – most inverts do not feature in studies of large-scale BD change. urgent need to mobilize existing data and interrogate them with modern, rigorous analysis tools. Determining drivers will aid mitigation of future losses.

Cardoso, 2020 – harder to quantify how rare species are responding. Beta diversity decreased by removing rare species and homogenizing rare species. Minimize problems with existing data by taking advantage of multiple datasets.

Hallmann, 2020 – info on abundance and trends of insects is largely lacking, and/or geographically limited. More data available for butterflies, dragonflies, bees, and moths, so also taxonomically limiting.

Lister and Garcia, 2018 – arthropods comprise over 2/3 of terrestrial species, but info on their abundance and extinction rates in tropical habitats is severely limited.

Habel, 2019 – use of large data sets and sophisticated statistical analyses can help disentangle drivers.

Dirzo, 2014 – invert biodiversity data are extremely limited. Less than 1% of the 1.4 million described invertebrate species have been assessed for threat by the IUCN, of those assessed, ~40% are considered threatened.

Homburg, 2019 – long term studies of insect diversity trends are still rare.

Fox, 2019 – imperfect sampling and short-term stochastic variation can lead to incorrect quantification of extinction risk (Red List). Assessment of insect taxa likely to be particularly prone to these problems as pops are highly dynamic. Inverts very different to vertebrates. 10 years may not be sufficiently reliable enough. Need longer time period for study to dampen the effects of annual variation.

Didham, 2020 – historical pop abundance rarely available so what should the baseline reference state be? Few studies can achieve complete census of all individuals. How far can you expand findings to population as a whole? Most biases (apart from shifting baseline) are likely to over-estimate reported cases of insect decline.

Montgomery, 2020 - we do not yet have the data to assess large-scale spatial patterns in the severity of insect trends. Geographically restricted studies. Only small fraction of insects have had any substantial pop monitoring. Most long-term pop data is from human-dominated landscapes in western and northern Europe. Need to understand how quicky pops are trending. Are rates on par with those of birds, plants, and mammals? How widespread? – especially need to know about tropics and southern temperate regions where most species occur.

Boyes, 2019 – multiple drivers may be involved, and drivers are poorly understood. Search for ecological traits associated with winners in needed.

Van Strien, 2019 – historic species occurrence is fragmentary. Not collected using standardised field protocols – opportunistic.

Wagner, 2021a – urgent need for more data to make robust conclusions.

Saunders, 2020 – insect apocalypse narrative is fueled by limited number of studies that are restricted geographically (UK, Europe, US) and taxonomically (bees, marolepidoptera, ground beetles). Sánchez-Bayo and Wyckhuys (2019) extrapolated beyond the limitations of their review to suggest evidence of global decline across all insect taxa – spread unchecked through media and in peer-reviewed articles uncritically as evidence for global-scale insect decline. Very limited knowledge of how multiple drivers impact insects across the whole of their life cycle.

Wepprich, 2019 - a fifth of regularly observed species in Ohio did not meet our minimum data requirements to for us to estimate trends.

Hudson, 2017 - need to model the response of local biodiversity to human pressures and, thus, to estimate biodiversity changes at local scales, but across a wide spatial domain (ideally globally) and for a wide range of taxa.

Millard, 2021 - most of the evidence on which these claims are made is patchy, based on studies with low taxonomic and geographic representativeness.

*Other:*

Wagner, 2021b – studies that generalize across datasets provide much needed perspective on e.g. general health of region's pollinators, often overlook species-level trends

Outhwaite, 2020 - care is needed to avoid the pitfalls of shifting baseline syndrome.

Homburg, 2019 – insects are most diverse taxon on Earth in terms of species numbers, beetles representing largest proportion. Identifying characteristics which are common in those species which declines may enhance our understanding of the drivers.

Brooks, 2012 - Studying species in isolation is unlikely to deliver a holistic understanding.

Didham, 2020 – high-inter annual variation is the norm rather than the exception. Poses problems in determining what the baseline reference state should be. Shifting baseline phenomenon.

Montgomery, 2020 – large natural fluctuations from year to year make it difficult. 80% of insects remain undescribed. Time/cost prohibitive to identify every insect. Need repeatable sampling methods. Biomass may be easier as does not require fine-scale taxonomic knowledge. Long-term time series data are especially valuable. Surveys across gradients would be good. Publish positive/stable trends as well as negative to overcome publication bias and aid meta-analyses. Ecosystem function and services may depend strongly on abundance of common species, more than number of species delivering the service.

Van Strien, 2019 - specimens of the most common species have often been ignored if enough specimens had already been collected. So, the increase of some common species is probably over-estimated.

Crossley, 2021 - what constitutes convincing evidence for global degradation of plant and animal biodiversity in the Anthropocene?

De Palma, 2015 – differential detectability – e.g. larger species that are active for longer are more likely to be sampled.

Millard, 2021 - More than 75% of the terrestrial world exhibits direct evidence of historical or current transformation24, with just over 50% (~67 million km²) currently used by humans25. Temperate non-tropical regions have a longer history of agricultural activity, which may have acted to filter more sensitive species, meaning more recent shifts towards intensive agriculture may have a smaller effect. What about extinction-debt effects?