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„Land-use legacies on agrobiodiversity  
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## **German Summary**

### *Einleitung*

Menschliche Gesellschaften und ihre Lebens- und Wirtschaftsformen beeinflussen terrestrische und aquatische Ökosysteme auf vielfältige Weise und resultieren oft in einem Rückgang von Biodiversität auf lokaler, regionaler und globaler Ebene (Worm et al. 2006; Butchart et al. 2010; Thomas 2013). Seit der industriellen Revolution, und insbesondere seit der 2. Hälfte des 20. Jahrhunderts ist die Intensivierung der Landnutzung ein Faktor (Foley et al. 2011; Krausmann et al. 2013), der besonders negative Effekte auf Artenreichtum hat (Sala et al. 2000). Die Habitate vieler Arten verschwinden aus industriell genutzten Agrarräumen oder erfahren zumindest erhebliche Flächenverluste und Fragmentierung. Das Aussterben der mit diesen Habitaten assoziierten Arten erfolgt jedoch oft mit Verzögerung. In der Fachliteratur wird der dadurch intermediär vorhandene „Artenüberschuss“ als „Extinction debt“ bezeichnet (Tilman et al. 1994; Kuussaari et al. 2009), die Zeit, bis diese Schuld abgetragen ist, als „Relaxation time“. Letztere ist unter anderem von der Lebenserwartung der Arten abhängig. Bei langlebigen Arten (z.B. ausdauernde Pflanzen) dauert es oft lange bis sich nach einer Veränderung der Lebensbedingungen ein neues Gleichgewicht zwischen Umwelbedingungen/Habitatverfügbarkeit und Artenzahlen eingestellt (z.B. Krauss et al. 2010). Bei kurzlebigen Organismen zeigen empirische Untersuchungen widersprüchliche Resultate (z.B. Krauss et al. 2010, Sang 2010). Das lässt vermuten, dass neben dem Ausmaß (Flächengröße) auch die Art und Intensität der Habitatveränderung großen Einfluss auf Auftreten und Ausmaß der Zeitverzögerung haben. Quantitativ und qualitativ intermediäre Veränderungen führen theoretisch zu den längsten Zeitverzögerungen (Hylander & Ehrlen 2013), da sie die meisten Arten betreffen, aber das Habitat nicht vollständig zerstören. Bis jetzt hat sich die Forschung der „Extinction debt“ eher auf Landschaften konzentriert, die große Anteile von naturnahen Flächen aufweisen oder wo im Agrarland solche Biotope erhalten geblieben sind. Zudem waren empirische Untersuchungen meist auf Arten beschränkt, die auf diese naturnahen Habitate spezialisiert sind (e.g. Krauss et al. 2010). Im Gegensatz dazu gibt es bis jetzt wenige wissenschaftliche Arbeiten zur „Extinction debt“ von Agrarbiodiversität im engeren Sinn, also von Arten, die Äcker und ihre Begleitbiotope als Lebensraum nutzen.

Ein großer Teil der zentraleuropäischen Landschaften wurde bereits vor Jahrzehnten, oft sogar Jahrhunderten, in landwirtschaftliche Flächen umgewandelt (Klein Goldewijk et al. 2011), mit einschneidenden Folgen für die Artenzusammensetzung und den Artenreichtum dieser Landschaften (z.B. Donald et al. 2001; Tscharntke et al. 2005). Die Veränderungen nach dem 2. Weltkrieg brachten eine noch intensivere Nutzungsweise (z.B. Dünger, Herbizide, Mechanisierung etc.) und einen stetigen Anstieg des vom Menschen aus den Ökosystemen entnommenen Anteils der natürlichen Netto-Primärproduktion (NPP, Wright 1990; Krausmann et al. 2003). Mit dieser steigenden Nutzungsintensität war oft eine klare räumliche Trennung der Landnutzungstypen verbunden (z.B. Feldfruchtproduktion im Gegensatz zu Viehwirtschaft), die in Kombination mit der räumlichen Bereinigung zerstreuter Besitzstrukturen zu einer Homogenisierung auf Landschaftsebene und einem massiven Verlust von Randbiotopen und linearen Grenzstrukturen (z.B. Hecken, Feldgehölze) führte. Insgesamt ist dadurch die Habitatdiversität auf Landschaftsebene stark zurückgegangen (Benton et al. 2003)

mit sehr wahrscheinlich negativen Effekten auf den Artenreichtum dieser Landschaften (Moser et al. 2002). Über Extinction debt und Relaxation time bei der Reaktion der Biodiversität auf solche Veränderungen ist allerdings wenig bekannt.

In dieser Arbeit untersuche ich solche zeitverzögerten Reaktionen der von Agrarbiodiversität auf rezente Landschaftsveränderungen anhand von 100 in Österreich liegenden Agrarlandschaften. Ich setze dazu den rezenten Artenreichtum von drei taxonomischen Gruppen (Gefäßpflanzen, Schmetterlingen und Heuschrecken) in diesen Landschaften mit der Veränderung der Landnutzungsintensität über mehrere Zeitpunkte in der zweiten Hälfte des 20. Jahrhunderts in Beziehung. Im Speziellen untersuche ich die drei folgenden Fragen: (i) Erklären die Landnutzungsintensität früherer Zeitpunkte die heutige Biodiversität besser als die aktuelle, was auf das Vorhandensein einer Zeitverzögerung schließen ließe? (ii) Wenn ja, unterscheiden sich die verschiedenen taxonomischen Gruppen in der Länge der zeitlichen Verzögerung, also zeigen (langlebige) ausdauernde Pflanzen längere Verzögerungen als (kurzlebige) Insekten? (iii) Zeigen einjährige Pflanzen kürzere Verzögerungen als ausdauernde Pflanzen?

### Methoden

In meiner Analyse konnte ich auf zwei bereits bestehende Datensätze zurückgreifen: zum einen eine Biodiversitätserfassung von 100 quadratischen Flächen (Seitenlänge: 625 m) in österreichischen Agrarlandschaften. Darin wurden Artenzahlen von Gefäßpflanzen, Schmetterlingen und Heuschrecken erhoben sowie die Landschaftsstruktur mit insgesamt 101 verschiedenen Habitattypen kartiert (Pascher et al. 2011). Zum anderen einen Datensatz zur historischen Entwicklung des Landnutzungsindikators „Human Appropriation of Net Primary Production“ (HANPP) in Österreich (Krausmann, 2001). HANPP misst den Anteil der NPP, der aufgrund menschlichen Handelns den Ökosystemen entzogen wird und bezieht dabei sowohl Änderungen der Landnutzung (z.B. Transformation einer natürlichen Waldfläche in Ackerland) als reale Biomassennahme (Ernte) mit ein (Haberl et al. 2007).

Basierend auf der Erhebung zur Landschaftsstruktur berechnete ich einen Index, der die Habitat-Diversität in diesen Landschafen beschreibt (Simpson's Landschaftsdiversitäts-Index, McGarigal & Marks 1995) für jede der 100 Testflächen für den Zeitpunkt der Aufnahmen (2007/08) mithilfe der Funktion „diversity“ des R-Pakets „vegan“ (Oksanen et al. 2013). Weiters berechnete ich einen HANPP Wert (in % der NPP der potentiellen natürlichen Vegetation, NPP<sub>pot</sub>) für jede der 100 Probeflächen für die Jahre, die der HANPP-Datensatz abdeckte (1949, 1959, 1969, 1979, 1986, 1990 und 1995): für das Jahr 1995 basierte dieser Wert auf einer Aggregation der 101 kartierten Habitattypen zu 9 Landnutzungsklassen, die mit bestimmten HANPP-Werten assoziiert sind (Tab. S1). Für die vorangehenden Jahre wurden Bezirks-weise erhobene Trends der historischen HANPP-Entwicklung auf diese Testflächen übertragen. Anschließend wurden diese HANPP-Trends in Trends der Landschaftsdiversitäts-Index-Werte umgerechnet (Tab. S2; Fig. 1 Inlet), da Landschaftsdiversität und Landnutzungsintensität eng zusammenhängen (Wrbka et al. 2004).

Um die Korrelation zwischen den Landschaftsdiversitäts-Werten (unabhängige Variable) und den Artenzahlen (abhängige Variable) zu analysieren, verwendete ich generalisierte lineare gemischte Modelle (GLMMs) für jedes Jahr; kalkuliert mit Hilfe des R-Pakets „lme4“ (Funktion „glmer“, Bates et al. 2013). Des weiteren berechnete ich auch

generalisierte lineare Modelle (GLMs) für jedes Jahr und jedes Taxon sowie einjährige bzw. ausdauernde Pflanzen, um Modelle für die Vergleiche der Taxa zu erhalten. Ich bewertete die Modelle anhand der Modellgüte (McFadden's  $R^2$ -Werte, McFadden 1979) für die GLMMs und D<sup>2</sup>-Werten (Guisan & Zimmermann 2000) für die GLMs bzw. mit Hilfe des Akaike Informations Kriterium (AIC) und den daraus berechneten „Akaike weights“ (R-paket „MuMIn“, Barton 2013). Da Artenzahlen und Landschaftsdiversität einen unimodalen Zusammenhang zeigten (Fig. S1) verwendete ich Polynome zweiter Ordnung für die Modellberechnungen.

### Ergebnisse

Die 100 Testflächen unterschieden sich im Aufnahmejahr 2007/08 deutlich in Bezug auf den Artenreichtum der Gefäßpflanzen, Schmetterlinge und Heuschrecken, in den Anteilen einjähriger und ausdauernder Pflanzen und auch in ihrer Landschaftsdiversität (Tab. 1, Details: Pascher et al. 2011).

Die HANPP Werte waren auf fasten allen Flächen ziemlich hoch, wie für mitteleuropäische Landschaften zu erwarten (Krausmann et al. 2012). Über den Erhebungszeitraum 1949 bis 1995 war im Durchschnitt kein markanter Trend festzustellen (Fig. S2), teils weil die Werte der individuellen Testflächen relativ stabil waren, teils weil deutliche Anstiege auf einzelnen Flächen durch deutliche Rückgänge auf anderen kompensiert wurden (Fig. 1).

Im Mittel aller drei taxonomischen Gruppen (GLMMs) erklärte die Landschaftsdiversität aus dem Jahr 1986 die Artenzahlen aus 2007/08 am besten; sowohl AIC als auch „Akaike weights“ (AW) deuten darauf hin (Fig. 2). Zusätzlich zeigte das 1986er Modell auch den höchsten McFadden's  $R^2$ -Wert (Tab. 2, Fig. S3), obwohl die Modellgüte der verschiedenen Modelle nicht dramatisch differierte. Die separate Analyse der drei Taxa zeigte unterschiedliche Ergebnisse (Fig. 3, Tab. 3, Fig S4–S5): Gefäßpflanzen wurden am besten vom Modell aus 1986 erklärt, Schmetterlinge am bestem vom Modell aus 1990 und für Heuschrecken konnte kein am besten erklärendes Modell identifiziert werden. Für die ausdauernden Pflanzen war wie für Gefäßpflanzen insgesamt das Modell mit Landschaftsdiversität von 1986 am besten erklärend, Artenreichtum der einjährigen Pflanzen konnte mittels Landschaftsdiversität überhaupt nicht erklärt werden.

### Diskussion

Empirische Studien zum Thema Extinction Debt suggerieren, dass zwischen Lebensraumveränderung und der vollständigen Realisierung des dadurch ausgelösten Biodiversitätsverlusts im Fall langlebiger Organismen mehrere Jahrzehnte oder sogar mehr als ein Jahrhundert liegen können (Vellend et al. 2006; Krauss et al. 2010; Sang et al. 2010; Dullinger et al. 2013). Im Gegensatz dazu legen meine Ergebnisse nahe, dass in österreichischen Agrarlandschaften Biodiversität sich relativ rasch an Veränderungen von Landschaftsstruktur/Habitatausstattung anpassen kann: innerhalb von etwa zwei Jahrzehnten im Fall mehrjähriger Gefäßpflanzen (22 Jahre) und Schmetterlinge (18 Jahre); und möglicherweise sogar noch rascher im Fall einjähriger Pflanzen und Heuschrecken.

Ein Grund für diese eher kurzen Relaxation times könnte der relativ große räumliche Maßstab meiner Analyse sein, da bei größeren Bezugsräumen (z.B. regionale im Vergleich zu lokaler Artenpools) eher solche Zeitverzögerungen festzustellen sind

(Cousins & Vanhoenacker 2011). Zusätzlich haben bisherige Studien sich auf Spezialisten bestimmter Habitate konzentriert (Kuussaari et al. 2009). Im Unterschied dazu, habe ich alle Arten, also Spezialisten sowie auch Generalisten in die Analysen miteinbezogen. Die wenigen Studien über „Extinction debt“, die intensiv genutzte Landschaften auf großem räumlichen Maßstab untersucht haben, brachten ähnliche Ergebnisse: zum Beispiel konnten Cousins & Eriksson (2008) den heutigen Artenreichtum in schwedischen Agrarlandschaften kaum durch historische Landnutzungsmuster erklären.

Bezüglich des Vergleichs der zeitlichen Verzögerungen zwischen den verschiedenen taxonomischen Gruppen konnten bei den einjährigen und ausdauernden Pflanzen bisherige Forschungsergebnisse bestätigt werden: das Ausmaß der Zeitverzögerung scheint von der Lebensdauer der Art abhängig zu sein (e.g. Vellend et al. 2006; Lindborg 2007). Zusätzlich kommen einjährige Pflanzen in Agrarökosystemen hauptsächlich in Feldern und ruderalen Habitaten vor (Marshall et al. 2003) und sind deshalb nicht so sehr von Agrarintensivierungsmaßnahmen betroffen wie ausdauernde Pflanzen und auch Tiere, die vor allem an die wenigen naturnahen Inseln gebunden sind (e.g. Marshall & Moonen 2002; Cousins & Eriksson 2008).

Für Heuschrecken konnte wie auch für einjährige Pflanzen kein am besten erklärendes Modell gefunden werden. Ich vermute daher, dass die Reaktionszeit dieser Gruppen kürzer ist als die 12 Jahre zwischen 1995 und der Biodiversitätserfassung 2007/08. Zusätzlich sind alle in Mitteleuropa vorkommenden Heuschrecken einjährige Arten und zeigen deshalb auch nur kurze Relaxation times (Kuussaari et al. 2009). Für Schmetterlinge ist in der Literatur Uneinigkeit bezüglich Zeitverzögerungen nach Habitatsveränderungen zu finden: es konnten sowohl sehr rasche (wenige Jahre, Krauss et al. 2010) als auch Jahrzehntelang (Sang et al. 2010) verzögerte Reaktionen des Artenreichtums auf Landschaftsveränderungen beobachtet werden. Die ca. 20 Jahre Verzögerung, die meine Ergebnisse nahelegen, liegen mitten in diesem Streubereich.

Zusammenfassend zeigen meine Ergebnisse, dass Artenreichtum bei ausdauernden Pflanzen und Schmetterlingen auf Veränderungen der Landnutzungsintensität in österreichischen Agrarlandschaften mit etwa zwei Jahrzehnten Verzögerung reagiert; einjährige Pflanzen und Heuschrecken mit weniger als 10 Jahren. Diese Resultate suggerieren, dass Agrarbiodiversität kürzere Relaxation times zeigt als die Flora und Fauna naturnaher Rest-Lebensräume der Kulturlandschaft. Das impliziert, dass zukünftige Intensivierung in solchen Landschaften (wo das überhaupt noch möglich ist) relativ unmittelbare Effekte auf viele taxonomische Gruppen haben wird und das Zeitfenster für Biodiversitäts-erhaltende Managementmaßnahmen (Wearn et al. 2012) eng ist. Folglich sollten Fördermittel und andere Regulationsmechanismen von landwirtschaftlicher Landnutzung sehr gut hinsichtlich ihrer Effekte auf Biodiversität geprüft werden, da die Zeit um mögliche schädliche Auswirkungen auszubessern limitiert ist.



# **MANUSCRIPT**

Title of Manuscript

„Land-use legacies on agrobiodiversity  
in Central European landscapes“

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## **Keywords**

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## **Introduction**

Human actions and their direct and indirect impacts on both terrestrial and aquatic ecosystems foster changes, and often a decline of biodiversity from local to global scales (Worm et al. 2006; Butchart et al. 2010; Thomas 2013). Among the drivers of these changes, land-use intensification, a still ongoing global trend (Foley et al. 2011; Krausmann et al. 2013), is commonly thought to have particularly negative effects on species richness (Sala et al. 2000). In Central Europe, intensification has a long history and often implies loss and increasing fragmentation of traditionally used semi-natural ecosystems and a reduction of landscape diversity associated with a respective decrease of habitats suitable to specialist species (Moser et al. 2002; Sauberer et al. 2004). However, the complete loss of species from such landscapes often lags considerably behind landscape transformation creating what has been called an extinction debt (Tilman et al. 1994; Kuussaari et al. 2009). From a conservation perspective, such time lags are important because, on the one hand, the consequences of environmental modifications might be underestimated (Lindborg & Eriksson 2004) while, on the other hand, they may open a window of conservation opportunities (Wearn et al. 2012).

The so-called relaxation time, i.e. the time until all pending extinctions have become realized, is meant to depend on the lifetime expectancy of species (Kuussaari et al. 2009). Indeed, long-lived species have often been found to take a particularly long time to reach a new equilibrium with the altered environmental conditions (e.g. Krauss et al. 2010), while empirical results for short-lived taxa, like many insects, are mixed (e.g. Sang et al. 2010) suggesting that factors other than life span may have additional impacts on the occurrence and magnitude of an extinction debt and on the duration of relaxation times. Among these factors, the magnitude of habitat alteration probably plays an important role with intermediate levels of habitat change likely producing the most important extinction debts (Hylander & Ehrlen 2013) because they affect a relatively large number of species without completely destroying their habitats. Typically, empirical studies have hence concentrated on landscapes where a particular proportion of mostly semi-natural habitat types have been transformed, particularly into agricultural land, but remnants of these habitats have been conserved. Extinction debt has then been evaluated with a focus on those species, which are specialists of the reduced habitat type (e.g. Krauss et al. 2010). By contrast, little empirical work has so far been done on possible time lags of agrobiodiversity responses per se.

In fact, a considerable proportion of Central European landscapes has already been transformed to agricultural land decades or even centuries ago (Klein Goldewijk et al. 2011) with well-known negative effects on agrobiodiversity (e.g. Donald et al. 2001; Tscharntke et al. 2005). Post-World-War II transformations of such landscapes involved a more intense usage in terms of e.g. manure and herbicide and had major impacts on the productivity of agroecosystems and the share of Net Primary Production (NPP) co-opted by humans (Wright 1990; Krausmann et al. 2003). Changes commonly included spatial separation of land-use types (e.g. crop production vs. livestock farming) and further landscape-scale homogenization fostered by regrouping of properties and

disappearance of boundary structures to create larger land parcels of uniform use. Overall, landscape-scale habitat diversity has hence decreased (Benton et al. 2003) with a likely negative effect on the total species richness of these landscapes (Moser et al. 2002). However, little is known on possible time lags involved in these biodiversity responses.

In this study, we explore such time lags of agrobiodiversity using a sample of 100 agricultural landscapes scattered across Austria. We do so by relating the current species richness of three taxonomic groups, vascular plants, butterflies and grasshoppers, across these landscapes to the changing intensity of land use across a sequence of time points spanning the second half of the 20<sup>th</sup> century. Specifically, we address the following questions: (i) Do land-use data of some more distant time point explain current biodiversity patterns better than those of the recent past hence suggesting an extinction debt? (ii) If so, do the particular groups differ in this respect, i.e. do (longer-lived) vascular plants show longer relaxation times than (shorter-lived) insects? (iii) And, related to the second point, do annual plants show shorter relaxation times, if any, than perennial plants? As indicators for land-use intensity we use information on the human appropriation net primary production (HANPP), which measures the combined effect of land-use change and biomass harvest on energy availability in ecosystems (Haberl et al. 2007), together with Simpson's landscape diversity index (McGarigal & Marks 1995).

## Material & Methods

### *Species richness and landscape diversity*

Our analysis uses an existing biodiversity dataset from a monitoring program of genetically modified plants (BINATS, Pascher et al. 2011). The data comprises 100 test areas (625 m by 625 m) randomly distributed across Austrian agricultural regions, i.e. across landscapes with a proportion of forests and settlements < 20%.

Species numbers of vascular plants, butterflies and grasshoppers were recorded using a mixture of a random point and a transect sampling setup. Into each of the 100 test areas, ten circles (radius: 20 m) were randomly placed. Sampling was then done along to 40 m transects (width: one meter) spanning these circles north/south and east/west. Butterflies and grasshoppers were recorded once in summer under clear-sky conditions; vascular plants twice (spring & late summer). Based on aerial photographs, the whole test areas were additionally mapped for habitat structures. All fieldwork was carried out in the years 2007 and 2008. More detailed information about data acquisition is available in Pascher et al. (2010; 2011).

Based on the mapped distribution of habitat structures, we calculated Simpson's landscape diversity index (McGarigal & Marks 1995) for each of the 100 test areas for the time point of the survey (2007/08) using the function "diversity" of the R-package "vegan" (Oksanen et al. 2013).

### *Calculation of human appropriation of net primary production (HANPP)*

The 'human appropriation of net primary production' (HANPP) is an integrated socio-ecological indicator measuring the combined effect of land use and biomass harvest on the availability of trophic energy in ecosystems (Haberl et al. 2007). From an ecological perspective, HANPP can be defined as the difference between the NPP of the potential natural vegetation ( $NPP_{pot}$ ) and the NPP remaining in ecosystems after harvest ( $NPP_{eco}$ ). That is, it provides a measure of the impact of human activities on the availability of trophic energy in ecosystems. From a societal perspective, it measures the combined effect of land-use induced changes in NPP ( $HANPP_{luc}$ ) and NPP extracted from ecosystems by biomass harvest for socioeconomic use ( $HANPP_{harv}$ ).

We used data from a study, which investigated the long-term historical development of HANPP parameters in Austria to calculate HANPP for the test areas (Krausmann, 2001). The dataset provides region specific information on land use and aboveground HANPP parameters in energy units (MJ) for the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995. NPP of six aggregated land-use types was estimated on the basis of detailed data from agriculture and forestry statistics and reflects both changes in land-cover and land-use intensity (yields) over time (see Krausmann 2001 for details). Subsequently, we pooled the 101 habitat types of the landscape maps of into the same aggregated land use types (Tab. S1) and calculated HANPP values (for the year 2007) for the 100 test areas. We then made two assumptions: (1) we assumed that the temporal HANPP-trend recorded and calculated at the level of political municipalities is representative of the temporal HANPP-trend of the test areas localized within these municipalities and hence interpreted these trends as indicators for the changing land-use intensity at these test areas across the seven time points; (2) as landscape diversity and land-use intensity are closely linked (Wrbka et al. 2004), we translated the HANPP-trend into a trend of the

landscape diversity index at each test area (Tab. S2). Put it another way: we used municipality-level trends in HANPP as an indicator of the change in land-use intensity at the test areas and quantified this trend by a change of the landscape diversity index across the seven time points (Fig. 1 inlet). This approach certainly involves inaccuracies due spatial downscaling and transfer among indices, but allows expressing larger-scale trends in land-use intensity (HANPP at municipality level) in terms of a currency that is relevant for species richness at smaller scales, i.e. habitat diversity at the scale of individual test areas.

#### *Data analysis*

To relate species richness with landscape diversity as a predictor we fitted generalized linear mixed-effects models (GLMMs) for each of the seven years using taxonomic group (vascular plants, butterflies, grasshoppers) as grouping variable. GLMMs were computed in R (R Core Team 2013) with the function “glmer” of the R-package “lme4” (Bates et al. 2013) with a log link function for Poisson distributions. As species richness and landscape diversity showed a unimodal correlation we used second-order polynomials of landscape diversity for model fitting. Model comparison was done by using Akaike weights (AW) calculated from the Akaike Information Criterion (AIC) using R-package “MuMIn” (Barton 2013). AW shows the probability that a model explains a given dataset best among a group of candidate models (Burnham & Anderson 2004). To evaluate the goodness of fit of the GLMMs we calculated McFadden’s  $R^2$ -values (McFadden 1979). The null models of the respective GLMMs were computed with the same random effect and an intercept term as the only fixed effect.

For taxon-specific analysis of the relation of species richness and landscape diversity, we additionally fitted generalized linear models (GLMs) for each of the seven years (1949–1995) and every taxonomic group as well as for annual vs. perennial vascular plants, respectively. Candidate GLMs were again compared by means of AWs. Goodness of model fit was evaluated by calculating explained deviance ( $D^2$ , Guisan & Zimmermann 2000).

## Results

Species richness of vascular plants, butterflies, grasshoppers as well as for annual vs. perennial vascular plants and Simpson's landscape diversity in 2007/08 varied strongly among the 100 test areas (Tab. 1, see Pascher et al. 2011 for details).

HANPP values were generally high as was expected for Central European agricultural areas (Krausmann et al. 2012). Temporal trends across the 100 test areas from 1949 to 1995 showed rather minor changes on average (Fig. 1). However, individual area trends varied considerably with part of the areas showing a rather pronounced increase or decline of HANPP, respectively (Fig. 1).

Across all three taxonomic groups, the models with Simpson's landscape diversity from 1986 provided the best explanation for the variation in species richness across the 100 landscapes in 2007/08. The difference in the Akaike information criterion (AIC) between the 1986-model and all six other models was consistently  $> 10$ , and hence all models except the one of 1986 have essentially no support (Burnham & Anderson 2004). Similarly, Akaike weights (AW) strongly suggested the 1986-model to be superior to those of all other time points (Fig. 2) even if landscape diversity was significantly linked to species richness patterns in all seven GLMMs. Accordingly, the model from 1986 also showed the highest McFadden's  $R^2$  value (Tab. 2), although goodness of model fit did not differ strongly among the models.

However, the separate analysis of each of the three taxonomic groups demonstrated pronounced variation among them (Fig. 3): while vascular plants are most responsive to the landscape diversity values of 1986, butterfly richness is better explained by the data from 1990 and grasshoppers did not show any clearly best fitting model. Among vascular plants, perennial species richness was again best explained by landscape diversity from 1986 while the distribution of annual plant richness could not be well explained by landscape diversity from any of the tested years. In terms of goodness of fit (Tab. 3), models explained a considerable amount of the variation of perennial vascular plant richness ( $D^2$  around 0.5), less of butterfly (around 0.25) and grasshopper richness (around 0.3), and next to no variation of annual plant species richness. As a corollary, the overall superiority of the 1986-model is mainly driven by the particularly high correlation of perennial vascular plants with the landscape diversity-distribution of this year. Similarly, GLMM random effects around 2.0 for vascular plants compared to values around -1.5 (butterflies) and -0.5 (grasshoppers) underline the major contribution of plants to the overall result of the GLMMs.

## Discussion

Recent studies have demonstrated that species-richness patterns of certain taxonomic groups lag significantly behind environmental deterioration with frequent lag times of several decades, or even longer (Vellend et al. 2006; Krauss et al. 2010; Sang et al. 2010; Dullinger et al. 2013). By contrast, our results suggest that species-richness patterns in Austrian agricultural landscapes reflect a legacy of only about two decades for perennial vascular plants (22 years) and butterflies (18 years), and probably even shorter ones for annual plants and grasshoppers.

As Cousins & Vanhoenacker (2011) showed, relaxation times depend on spatial scales and tend to increase when switching from  $\alpha$ - (local to landscape scale) to  $\gamma$ -diversity (regional scale). One reason for the rather short time lags suggested by our results might hence be the relatively small spatial scale of our study areas (i.e. 100 test areas with 625 m by 625 m). In addition, while most empirical studies have focussed on specialist species of certain habitat types, our approach used the overall species richness of landscapes including both generalist and specialist species, which might mask an extinction debt of species adapted to particular, decreasing, habitat types (Kuussaari et al. 2009). Finally, intensification of agricultural landscapes with initially small numbers of species inhabiting the rare remnants of low-intensity habitat types is likely to have more immediate consequences for diversity than only partial transformation of once larger semi-natural grasslands into croplands. Indeed, Cousins (2009) has shown that in landscapes with < 10% of remaining traditionally used grasslands signals of extinction debt tend to vanish. Indeed, the few other studies on extinction debt, which have focussed on small spatial scales in landscapes with intensive land-use regimes so far, provided comparable results. For example, Cousins & Eriksson (2008) concluded that past landscape patterns only weakly explain present-day species richness in Swedish agricultural landscapes.

Concerning comparison of relaxation times among taxonomical groups, differences among annual and perennial vascular plants confirm prior findings that underpin the dependency of such time lags on life time expectancy (e.g. Vellend et al. 2006; Lindborg 2007). In addition, annual plant species in agricultural landscapes occur predominantly in fields or ruderal habitats (Marshall et al. 2003) and are therefore presumably less susceptible to land-use intensification than perennial plant species or animal species whose occurrence is largely tied to remnant semi-natural habitats and extensive grasslands (e.g. Marshall & Moonen 2002; Cousins & Eriksson 2008). This difference in habitat preference may also explain why the models for annual plants did only poorly explain variations in species richness.

Similar to annual plants, our analyses did not suggest one specific best explaining model for diversity patterns of grasshoppers. The most likely explanation is, again, that a possible extinction debt has already been paid in the 12 years between 1995 and the species survey in 2007/08. Indeed, all Central European grasshoppers have annual life cycles and are hence expected to have short relaxation times, too (Kuussaari et al. 2009). Complementarily, Racz et al. (2013) have recently shown that grasshoppers recolonize restored grasslands with a delay of few years only, supporting the assumption that grasshoppers respond rapidly to habitat alterations in terms of both extinction and (re)colonization. Finally, the empirical evidence of extinction debt and relaxation times of butterfly species is mixed, with studies suggesting time lags of few years (Krauss et al.

2010) to several decades (Sang et al. 2010). A relaxation time of 18 years, as suggested by our study, is hence broadly within the range of what has been found so far.

We concede that the approach we have used is based on two important assumptions regarding the representativeness of larger-scale trends for the land use of individual landscapes and the transferability of HANPP-based indices of land-use intensity to a metric of landscape-scale habitat diversity. However, we point out that this approach should have fostered the superiority of the most recent models (where actual landscape configuration is most similar to the mapped one) if back-projection of habitat diversity trends would have introduced major errors. In fact, the most recent model of 1995 was the best explaining for none of the tested taxonomic groups strengthening our confidence that downscaling and index transformation have depicted actual trajectories in land-use intensity at the individual sites in broadly correct way. It might, however, be that differences among models would have been even more pronounced if a more precise measure of land-use history would have been available. In addition, HANPP values as a percentage of NPP of potential vegetation ( $NPP_{pot}$ ) might not have been the most sensitive proxy of land-use alterations, as HANPP in Central European agroecosystems has been raised to high levels due to deforestation prior to the 19<sup>th</sup> century and remained rather stable in the second half of the 20<sup>th</sup> century (Krausmann et al. 2012). Instead the use of a more dynamic indicator such as the ratio of NPP harvested by humans ( $HANPP_{harv}$ ) to  $NPP_{pot}$  (e.g. Dullinger et al. 2013) might provide a more distinctive trend of land-use intensity of the respective test areas.

In conclusion, our results suggest that overall species richness of perennial vascular plants and butterflies responds to changes in land-use intensity with a delay of about two decades in Austrian agricultural landscapes while annual plants and grasshoppers likely have relaxation times < 10 years. These findings underpin that agrobiodiversity tends to show relaxation times shorter than species specifically adapted to semi-natural habitats. This implies that future intensification of such landscapes (where this is still possible) will have rather immediate effects with an only narrow “window of conservation opportunity” (Wearn et al. 2012) for many taxonomic groups. As a corollary, subsidies and other schemes meant to regulate agricultural land use should take particular care of their effects on biodiversity, as the time for correcting detrimental impacts is limited.

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## Figures

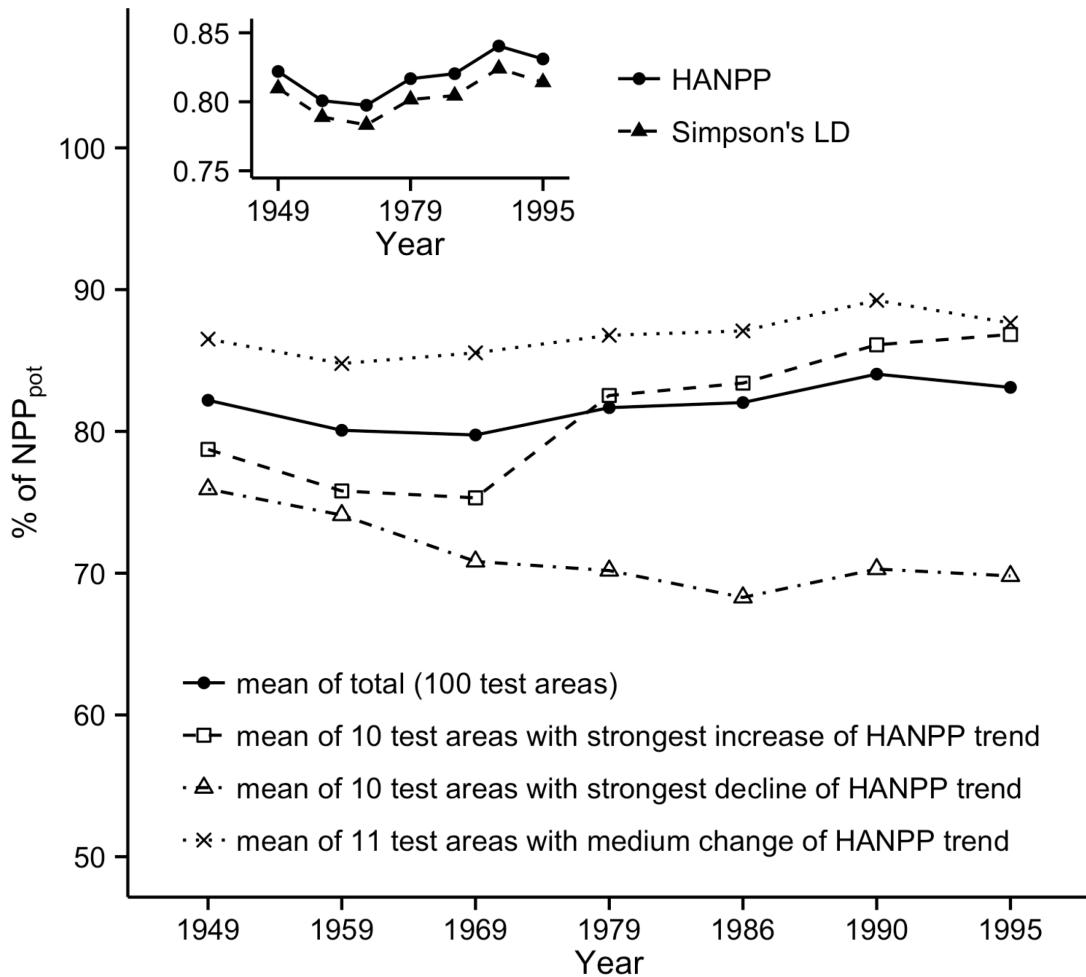


Figure 1: Change of human appropriation of NPP (HANPP) for the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 as a percentage of NPP of potential vegetation ( $NPP_{pot}$ ). Continuous line & filled circles show the mean of the 100 test areas. Dashed line & squares show the mean of 10 test areas with strongest increase, dotted line & triangles show the mean of 10 test areas with strongest decline, and dashed-dotted line & crosses show the mean of 11 test areas with medium change of HANPP, calculated by fitting a linear model for each test area (with HANPP as a response and time as a predictor) and ordering the areas by ranking the slopes of the respective linear models. Inlet plot: Means of HANPP and Simpson's landscape diversity of the 100 test areas for the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995. HANPP (continuous line & filled circles) is shown as a percentage of  $NPP_{pot}$ . Landscape diversity (dashed line & filled triangles) values were calculated by transforming HANPP trends for each test area separately.

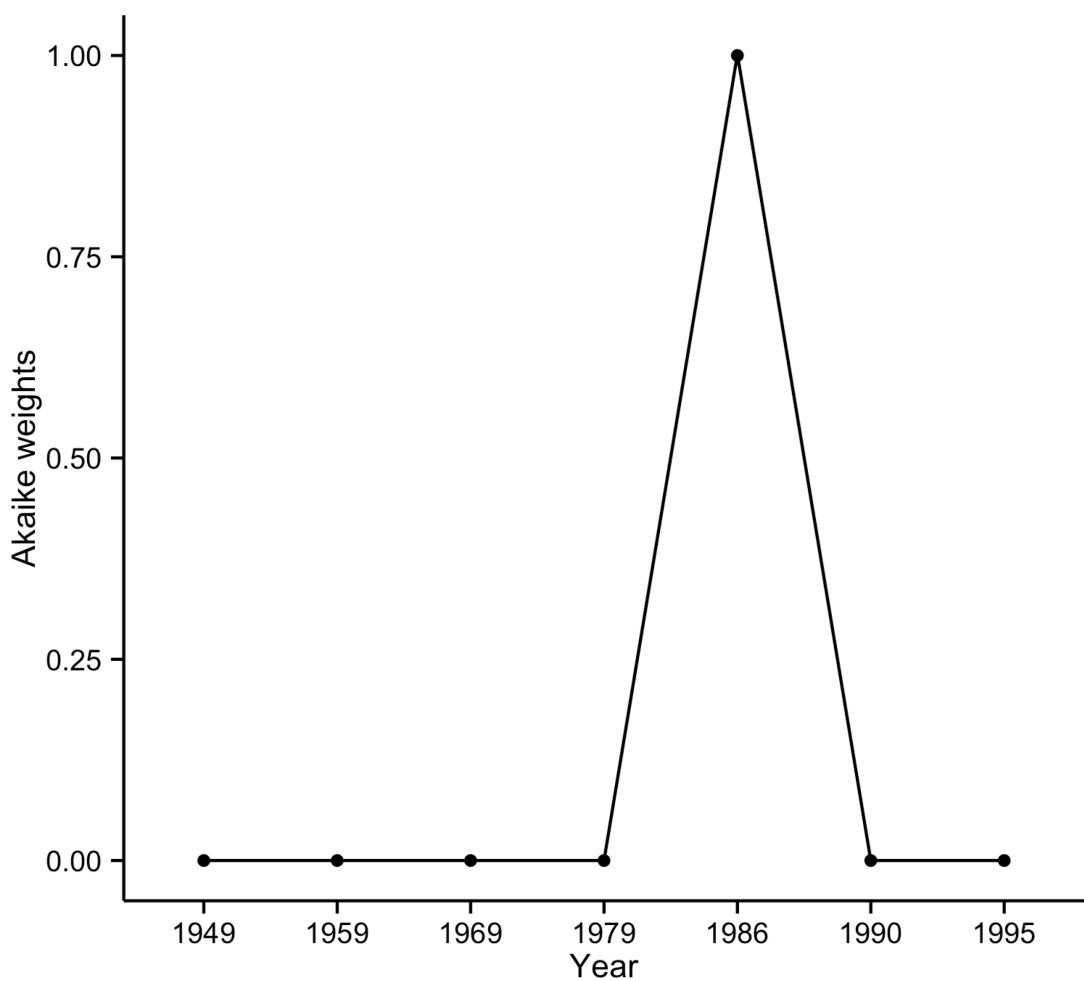


Figure 2: Relative support (Akaike weights) for generalized linear mixed models (GLMMs) explaining the species richness of 2007/08 of all 3 taxonomic groups together (vascular plants, butterflies, and grasshoppers) using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995.

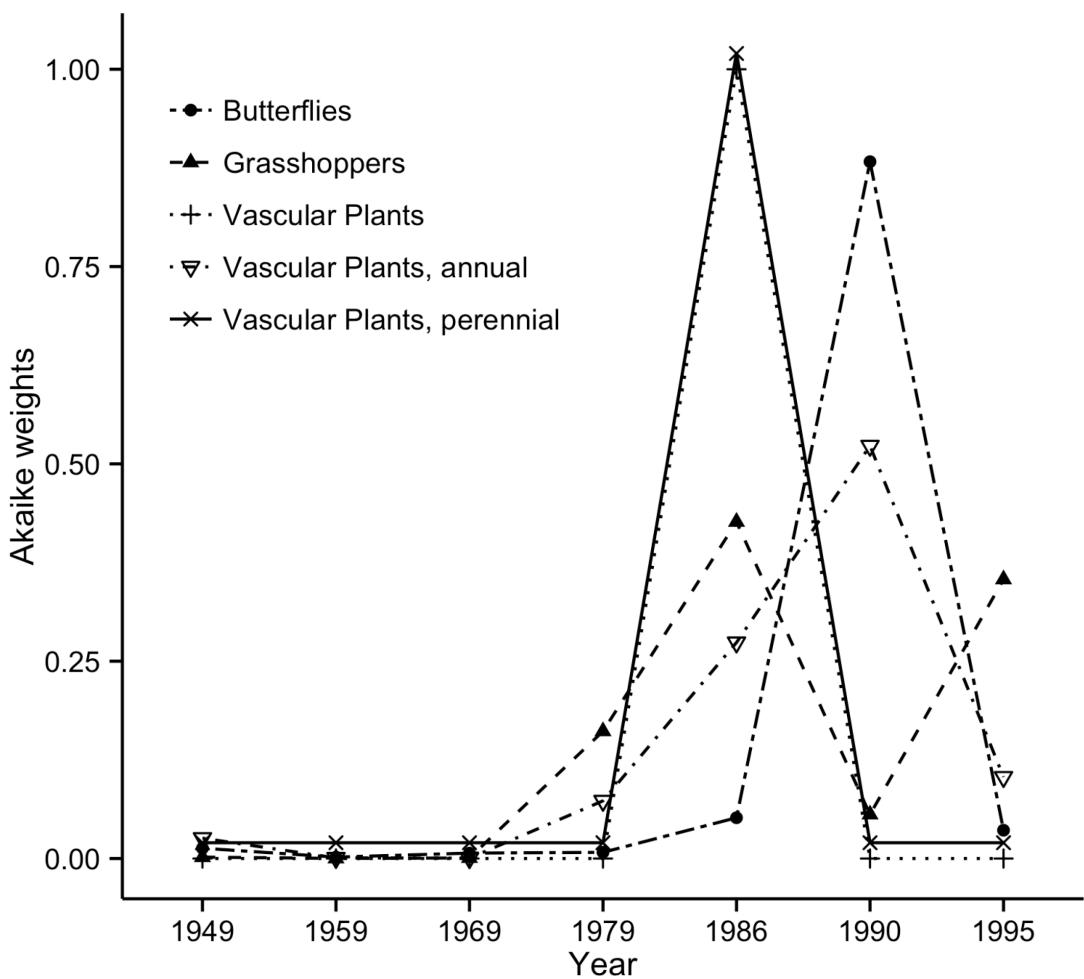


Figure 3: Relative support (Akaike weights) for generalized linear models (GLMs) explaining the species richness of 2007/08 of butterflies, grasshoppers, vascular plants, annual and perennial vascular plants using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 as predictor variables. Butterflies: two-dashed line & filled circles; grasshoppers: dashed line & filled triangles; vascular plants: dotted line & pluses; vascular plants, annual: dot-dashed line & triangles point down; vascular plants, perennial: jittered +0.02, continuous line & crosses.

## Tables

Table 1: Summary table of species richness and Simpson's landscape diversity in 2007/08.

	mean	max	min
Butterflies	4	15	0
Grasshoppers	10	21	1
Vascular Plants	115	212	22
Vascular Plants, annual	46	101	15
Vascular Plants, perennial	58	153	1
Simpson's Landscape Diversity	0.81	0.94	0.26

Table 2: Akaike information criterion (AIC) values for model comparison and McFadden's  $R^2$  values showing goodness of model fit for generalized linear mixed models (GLMMs) explaining the species richness of 2007/08 of all 3 taxonomic groups together (vascular plants, butterflies, and grasshoppers) using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 as predictors.

Year	AIC	$R^2_{MF}$
1949	1542	0.32
1959	1568	0.31
1969	1542	0.32
1979	1407	0.38
1986	1323	0.41
1990	1427	0.37
1995	1351	0.40

Table 3: Akaike information criterion (AIC) values for model comparison and explained deviance  $D^2$  values as indicator for goodness of model fit for generalized linear models (GLMs) explaining the species richness of 2007/08 of butterflies, grasshoppers, vascular plants, as well as annual and perennial vascular plants using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 as predictor variables.

Year	Butterflies		Grasshoppers		Vascular Plants		Vascular Plants, annual		Vascular Plants, perennial	
	AIC	$D^2$	AIC	$D^2$	AIC	$D^2$	AIC	$D^2$	AIC	$D^2$
1949	485	0.18	580	0.25	1777	0.35	1060	0.04	1963	0.44
1959	489	0.16	585	0.23	1796	0.34	1067	0.03	1949	0.44
1969	486	0.17	582	0.24	1775	0.36	1068	0.03	1943	0.45
1979	486	0.17	571	0.29	1653	0.43	1058	0.05	1763	0.52
1986	482	0.19	569	0.30	1574	0.47	1056	0.05	1636	0.57
1990	476	0.21	573	0.28	1676	0.41	1054	0.06	1846	0.49
1995	483	0.19	569	0.30	1601	0.46	1058	0.05	1668	0.56

# APPENDIX

## Additional Figures & Tables

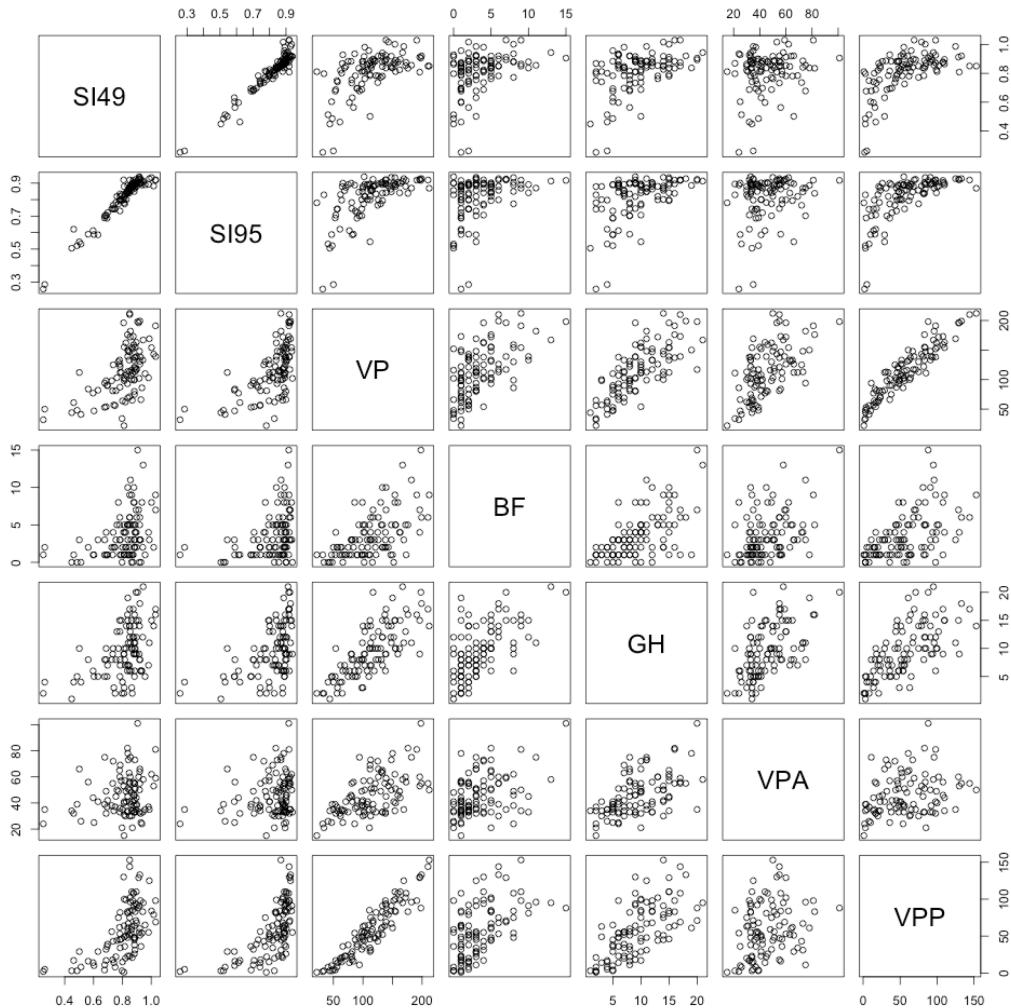


Figure S1: Scatter-plot matrix showing pairwise correlations for GLMM/GLM response variables (SI49 & SI95: Simpson's landscape diversity 1949 & 1995) and predictor variables (VP: vascular plants; BF: butterflies; GH: grasshoppers; VPA: vascular plants, annual; VPP: vascular plants, perennial).

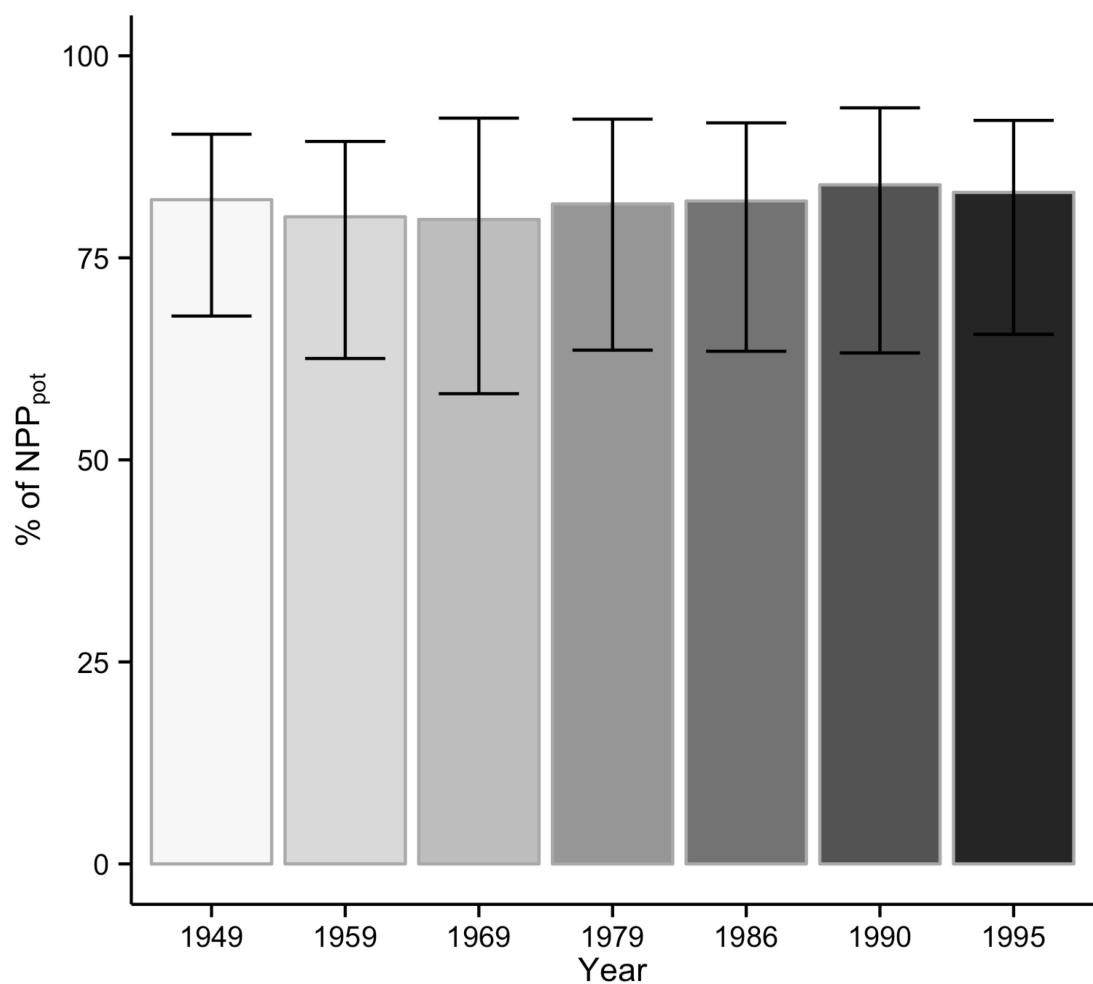


Figure S2: Mean values of human appropriation of NPP (HANPP) from the 100 test areas for the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 (light grey to dark grey) as a percentage of NPP of potential vegetation (NPP<sub>pot</sub>). Error bars show confidence intervals (95%) of the sample.

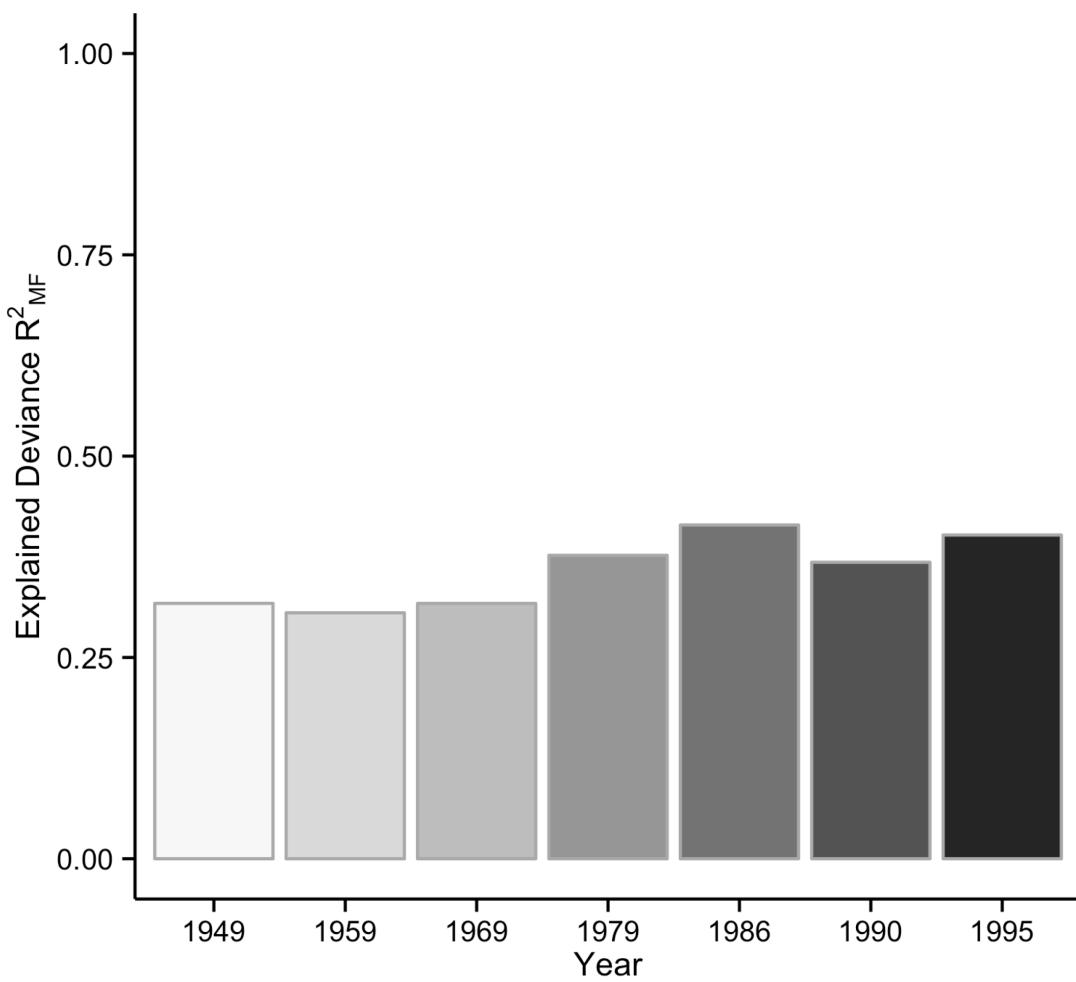


Figure S3: Goodness of model fit of the generalized linear mixed models (GLMMs) shown as McFadden's  $R^2$  values. GLMMs explaining the species richness of 2007/08 of all three taxonomic groups together (vascular plants, butterflies, and grasshoppers) using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 (light grey to dark grey).

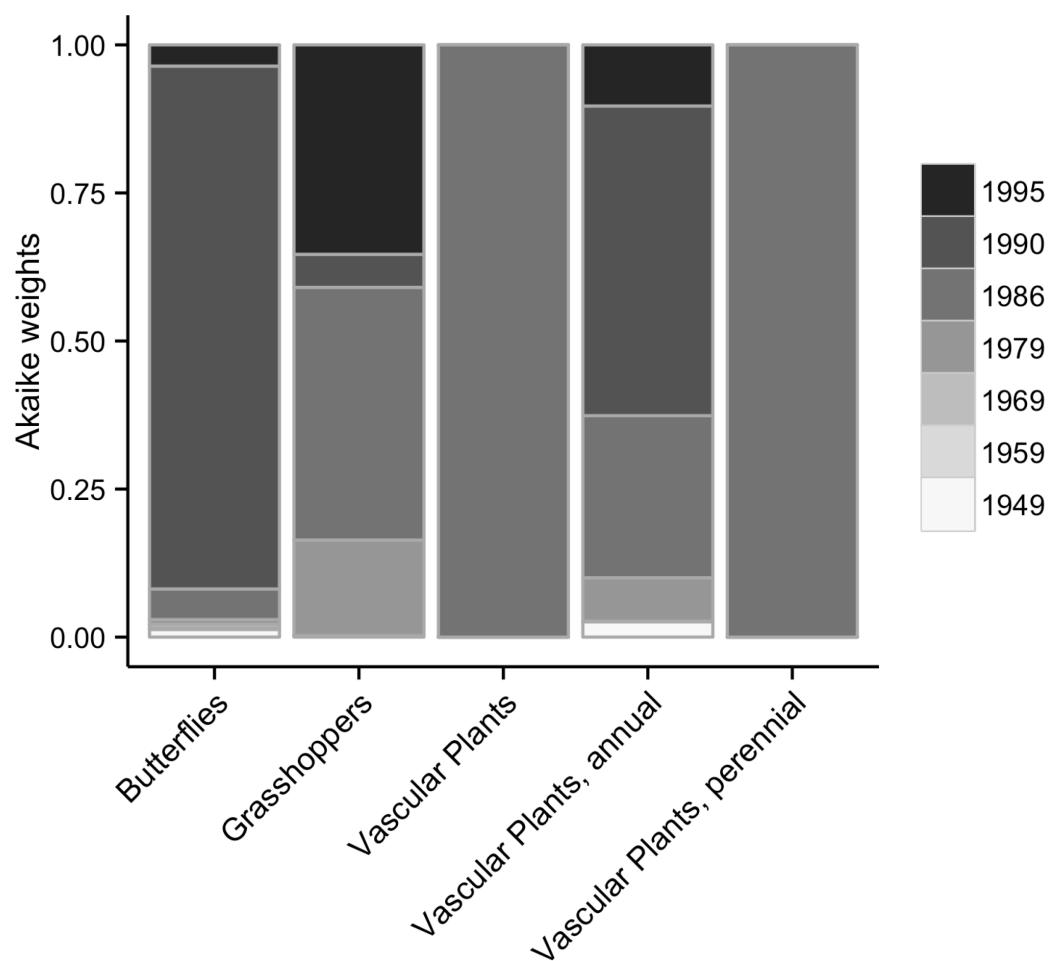


Figure S4: Relative support (Akaike weights) for generalized linear models (GLMs) explaining the proportions of species-richness patterns of 2007/08 (for butterflies, grasshoppers, vascular plants, as well as annual and perennial vascular plants) either by Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, or 1995 (light grey to dark grey).

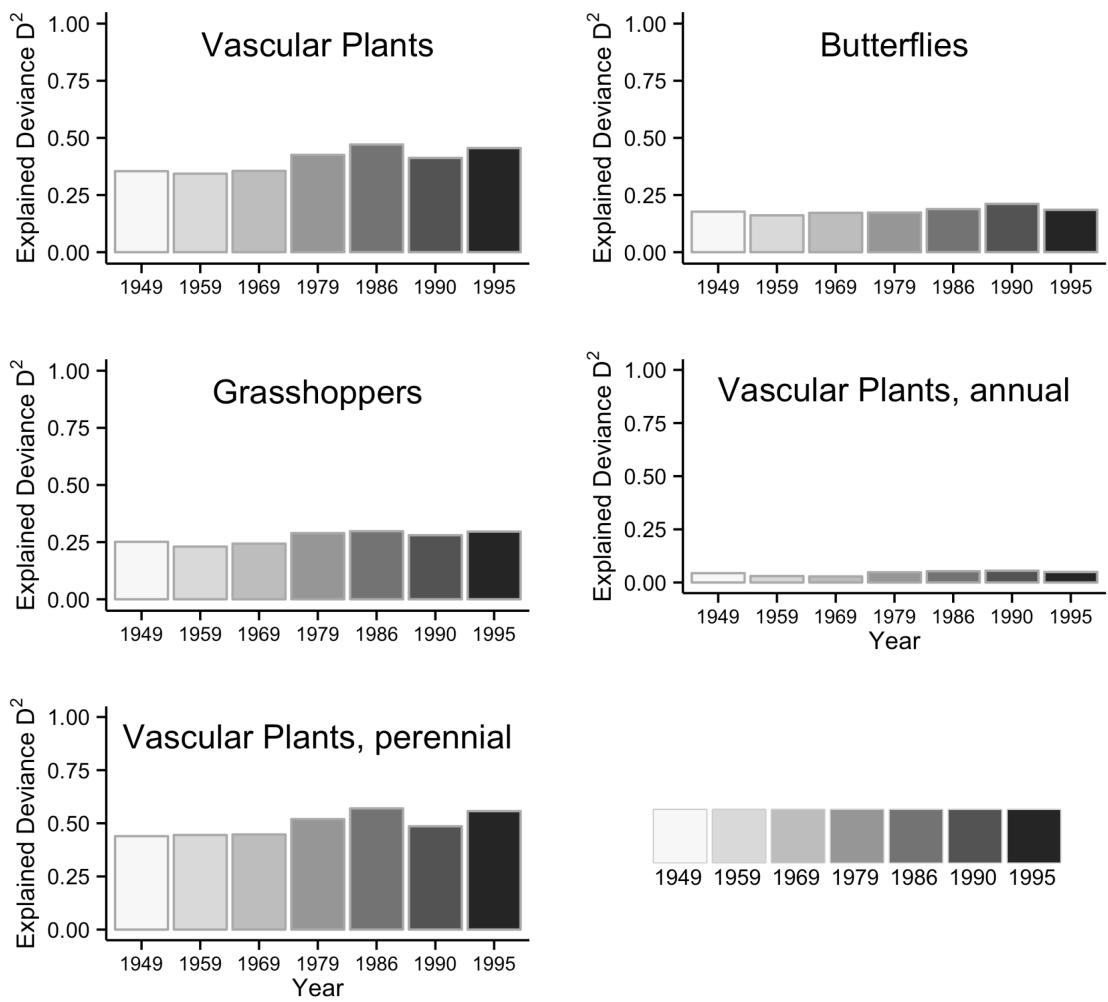


Figure S5: Explained deviance  $D^2$  as indicator for goodness of model fit for generalized linear models (GLMs) explaining the species richness of 2007/08 of butterflies, grasshoppers, vascular plants, as well as annual and perennial vascular plants using Simpson's landscape diversity from the years 1949, 1959, 1969, 1979, 1986, 1990, and 1995 as predictor variables (light grey to dark grey).

Table S1: Aggregation of 101 habitat structure types from the BINATS survey to nine land-use classes used for the HANPP calculation: bodies of water (Wasser), built-up areas (Siedlung), fallow land (Brache), fields (Acker), gardens (Garten), meadows (Wiesen), natural/semi-natural areas (Naturnahe), pastures (Weide), and woodland (Wald).

101 BINATS habitat structure types	9 aggregated land-use classes
streams and rivers	bodies of water
natural lakes and ponds	bodies of water
semi-natural man-made standing waterbodies	bodies of water
non-natural man-made standing waterbodies	bodies of water
dominated by shrubs	built-up areas
dominated by grasses	built-up areas
dominated by ruderals	built-up areas
ruderal flora of fresh conditions with open pioneer vegetation	built-up areas
ruderal flora of fresh conditions with closed vegetation	built-up areas
ruderal flora of dry conditions with open pioneer vegetation	built-up areas
ruderal flora of dry conditions with closed vegetation	built-up areas
non-natural hedges	built-up areas
fruit tree	built-up areas
line of fruit trees	built-up areas
old tree stand in parks and gardens	built-up areas
group of fruit trees	built-up areas
orchard meadows	built-up areas
scree	built-up areas
cliff (unconsolidated rocks)	built-up areas
temporary waterbodies	built-up areas
ditch	built-up areas
dyke	built-up areas
excavation sites	built-up areas
landfill and heaps	built-up areas
recreational and green areas	built-up areas
areas used as gardens	built-up areas
tarmac roads	built-up areas
gravel roads	built-up areas
track with herbaceous or grassy strips	built-up areas
herbaceous / grassy tracks	built-up areas
railway	built-up areas
buildings	built-up areas
poles and stations	built-up areas
small architectural constructions	built-up areas
residential area	built-up areas
areas of waste management	built-up areas
agricultural dump sites	built-up areas
fallow arable land	fallow lands
annual	fallow lands
2 to 5 years	fallow lands

101 BINATS habitat structure types	9 aggregated land-use classes
5 years and longer	fallow lands
intensively managed fields	fields
fields for game browsing	fields
forage crops	fields
elephant grass	fields
extensively managed fields with average habitat conditions	gardens
field with waterlogged habitat conditions	gardens
field with saline habitat conditions	gardens
vineyard	gardens
fallow vineyard	gardens
hop field	gardens
tree nurseries	gardens
fruit tree plantation	gardens
berry plantation	gardens
moist to waterlogged meadow	meadows
fresh meadow	meadows
dry meadow	meadows
reed-bed	natural areas
semi-xeric and xeric grassland	natural areas
fallow xeric grassland	natural areas
moist to waterlogged pasture	pastures
moist to waterlogged fallow land	pastures
fresh pasture	pastures
fresh fallow land	pastures
dry fallow land	pastures
shrub-rich field margin	pastures
field margin with grassland species	pastures
field margin with ruderal species	pastures
tall herb and grass communities	woodland
flora of felled areas	woodland
dwarf-shrub heathland	woodland
hedge with shrubs	woodland
hedge with trees	woodland
semi-natural gallery forest	woodland
non-natural gallery forest	woodland
deciduous trees	woodland
coniferous trees	woodland
mixed forest	woodland
deciduous tree	woodland
single bush and shrubbery	woodland
line of deciduous trees	woodland
line of coniferous trees	woodland
line of deciduous and coniferous trees	woodland

101 BINATS habitat structure types	9 aggregated land-use classes
group of trees	woodland
group of deciduous trees	woodland
group of coniferous trees	woodland
shrubbery of water-logged and moist habitat conditions	woodland
shrubbery of fresh habitat conditions	woodland
wood pastures	woodland
softwood alluvial forests	woodland
hardwood alluvial forests	woodland
alluvial forests with coniferous trees	woodland
scree and ravine forests	woodland
mixed Oak forests and Oak-Hornbeam forests	woodland
Beech forests and Spruce-Fir-Beech forests	woodland
Ash and Maple dominated deciduous forest	woodland
coniferous afforestation	woodland
deciduous afforestation	woodland
deciduous and coniferous mixed afforestation	woodland
pioneer forest	woodland
riparian pioneer habitats of standing waterbodies	woodland

Table S2: Translation of the HANPP-trend into a trend of the landscape diversity index at each of the 100 test areas. With the assumption that landscape diversity (LD) of 2007 equals landscape diversity of 1995 we calculated a factor describing the relation of LD 2007 and HANPP 1995 ( $LD\ 2007 / HANPP\ 1995 = Factor$ ). Subsequently, we calculated LD values for every year with this factor ( $HANPP\ year * Factor = LD\ year$ ).

Test area	LD 2007	Factor	HANPP 1986	HANPP 1990	HANPP 1995	LD 1986	LD 1990	LD 1995
1	0.83	0.0094	88.75	84.4	88.91	0.83	0.79	0.83
2	0.92	0.0105	88.67	78.23	87.72	0.93	0.82	0.92
3	0.9	0.0109	82.85	78.75	82.81	0.9	0.86	0.9
4	0.82	0.0093	87.23	84.42	88.58	0.81	0.78	0.82
5	0.94	0.0106	87.22	89.83	88.31	0.93	0.96	0.94
6	0.74	0.0081	91.56	93.46	91.75	0.74	0.76	0.74
7	0.9	0.0124	69.62	72.07	72.93	0.86	0.89	0.9
8	0.84	0.0096	87.11	91.87	87.38	0.84	0.88	0.84
9	0.8	0.0103	76.3	78.39	77.98	0.78	0.8	0.8
10	0.88	0.0133	68.4	69.41	66.18	0.91	0.93	0.88
11	0.9	0.0101	88.22	89	89.23	0.89	0.9	0.9
12	0.92	0.0108	83.28	84.79	84.93	0.9	0.91	0.92
13	0.93	0.0102	91.47	92.24	91.91	0.93	0.94	0.93
14	0.75	0.01	73.81	76.04	74.51	0.74	0.76	0.75
15	0.84	0.0093	90.35	93.45	90.9	0.84	0.86	0.84
16	0.85	0.0092	91.89	93.65	92.19	0.84	0.86	0.85
17	0.9	0.0118	73.18	76.93	76.69	0.86	0.91	0.9

Test area	LD 2007	Factor	HANPP 1986	HANPP 1990	HANPP 1995	LD 1986	LD 1990	LD 1995
18	0.82	0.0093	87.7	89.76	88.52	0.81	0.83	0.82
19	0.26	0.003	85.59	87.73	86.44	0.26	0.26	0.26
20	0.77	0.0084	92.05	93.9	92.25	0.77	0.79	0.77
21	0.77	0.0093	77.39	88.76	81.97	0.72	0.83	0.77
22	0.28	0.0032	87.16	89.36	89.2	0.28	0.29	0.28
23	0.86	0.011	75.91	78.39	78	0.83	0.86	0.86
24	0.8	0.0091	87.2	90.55	87.99	0.79	0.82	0.8
25	0.79	0.009	86.09	90.72	87.87	0.78	0.82	0.79
26	0.89	0.0181	49.97	48.05	49.28	0.91	0.87	0.89
27	0.89	0.0098	90.59	92.46	90.83	0.89	0.91	0.89
28	0.92	0.0107	85.13	88.5	85.92	0.91	0.94	0.92
29	0.84	0.0102	86.92	84.04	82.42	0.88	0.85	0.84
30	0.51	0.0056	87.88	89.36	89.42	0.5	0.5	0.51
31	0.7	0.0081	84.57	87.51	86.96	0.68	0.71	0.7
32	0.88	0.0104	85.75	88.57	84.5	0.89	0.92	0.88
33	0.9	0.0111	77.22	80.23	80.39	0.86	0.89	0.9
34	0.52	0.0063	79.23	79.57	82.2	0.5	0.5	0.52
35	0.88	0.0102	85.45	89.93	86.1	0.87	0.92	0.88
36	0.9	0.0107	82.43	83.97	84.28	0.88	0.9	0.9
37	0.69	0.0087	77.15	81.59	78.97	0.67	0.71	0.69
38	0.7	0.0086	79.59	80.38	81.57	0.68	0.69	0.7
39	0.54	0.0062	86.6	87	87.72	0.54	0.54	0.54
40	0.8	0.0097	81.23	85.95	82.17	0.79	0.84	0.8
41	0.74	0.0091	80.58	82.75	81.44	0.74	0.76	0.74
42	0.71	0.0082	83.44	84.28	86.63	0.68	0.69	0.71
43	0.69	0.0075	91.18	91.91	91.78	0.68	0.69	0.69
44	0.89	0.0129	66.28	65.69	68.85	0.86	0.85	0.89
45	0.88	0.0108	80.32	83.92	81.35	0.87	0.91	0.88
46	0.85	0.0101	83.45	86.33	84.87	0.84	0.87	0.85
47	0.87	0.0099	86.99	87.8	88.04	0.86	0.87	0.87
48	0.59	0.0075	77.71	78.57	78.76	0.58	0.59	0.59
49	0.92	0.0107	88.09	88.73	85.89	0.94	0.95	0.92
50	0.9	0.0117	76.22	75.89	76.5	0.89	0.89	0.9
51	0.92	0.0106	85.69	88.72	86.97	0.91	0.94	0.92
52	0.78	0.0087	88.75	90.46	89.56	0.78	0.79	0.78
53	0.89	0.0103	87.71	86.93	86.56	0.9	0.89	0.89
54	0.86	0.0099	86.23	89.2	87.55	0.85	0.88	0.86
55	0.89	0.01	88.91	90.38	89.12	0.89	0.9	0.89
56	0.83	0.01	81.8	84.71	83.1	0.82	0.85	0.83
57	0.93	0.0107	85.88	88.86	86.65	0.92	0.95	0.93
58	0.88	0.0099	87.85	90.81	89.06	0.87	0.9	0.88
59	0.82	0.0091	88.7	91.96	89.72	0.81	0.84	0.82
60	0.85	0.0097	86.23	88.78	87.27	0.84	0.86	0.85

Test area	LD 2007	Factor	HANPP 1986	HANPP 1990	HANPP 1995	LD 1986	LD 1990	LD 1995
61	0.91	0.0131	66.86	69.08	69.51	0.88	0.91	0.91
62	0.61	0.007	84.72	87.54	86.94	0.6	0.62	0.61
63	0.89	0.0112	79.51	84.39	79.52	0.89	0.94	0.89
64	0.9	0.0109	84.13	86.24	83.06	0.92	0.94	0.9
65	0.92	0.0114	81.2	84.18	80.99	0.93	0.96	0.92
66	0.9	0.0099	90.84	92.25	90.88	0.9	0.91	0.9
67	0.8	0.01	77.45	79.85	79.78	0.77	0.8	0.8
68	0.89	0.0103	85.17	87.84	86.35	0.87	0.9	0.89
69	0.89	0.01	89.21	90.78	89.05	0.89	0.91	0.89
70	0.62	0.0068	70.28	71.51	91.04	0.48	0.49	0.62
71	0.53	0.0059	89.15	90.99	89.53	0.53	0.54	0.53
72	0.86	0.0093	91.84	92.61	92.09	0.85	0.86	0.86
73	0.93	0.0129	71.24	74.62	72.14	0.92	0.96	0.93
74	0.72	0.0079	89.06	89.31	90.94	0.71	0.71	0.72
75	0.8	0.0087	90.67	92.47	91.61	0.79	0.81	0.8
76	0.92	0.0139	65.28	66.73	65.92	0.91	0.93	0.92
77	0.9	0.0104	86.36	89.39	86.42	0.89	0.93	0.9
78	0.77	0.0103	73.01	75.01	75.08	0.75	0.77	0.77
79	0.83	0.0092	90.53	91.72	90.23	0.83	0.84	0.83
80	0.92	0.0131	69.67	76.31	70.31	0.91	1	0.92
81	0.59	0.0067	88.59	95.05	87.75	0.59	0.64	0.59
82	0.9	0.0107	83.93	88.11	84.3	0.9	0.94	0.9
83	0.87	0.0111	78.77	81.93	78.12	0.88	0.91	0.87
84	0.78	0.012	61.76	61.01	65.18	0.74	0.73	0.78
85	0.88	0.0102	86.47	89.51	86.5	0.88	0.91	0.88
86	0.89	0.0101	87.11	91.06	87.47	0.88	0.92	0.89
87	0.87	0.011	78.99	79.51	78.8	0.87	0.88	0.87
88	0.92	0.0104	88.91	89.97	88.63	0.93	0.94	0.92
89	0.88	0.01	88.27	89.66	87.9	0.88	0.9	0.88
90	0.87	0.011	77.1	80.71	78.76	0.85	0.89	0.87
91	0.84	0.0108	77.8	80.97	78	0.84	0.87	0.84
92	0.74	0.0088	85.02	89.41	84.68	0.75	0.78	0.74
93	0.86	0.01	84.77	88.64	85.65	0.85	0.89	0.86
94	0.59	0.0101	54.64	55.47	58.2	0.55	0.56	0.59
95	0.89	0.0127	68.5	70.97	70.48	0.87	0.9	0.89
96	0.85	0.0118	70.73	72.46	72.17	0.83	0.85	0.85
97	0.73	0.0099	72.66	75.1	74.13	0.72	0.74	0.73
98	0.87	0.0097	89.69	92.92	89.63	0.87	0.9	0.87
99	0.89	0.0113	78.02	82.59	78.95	0.88	0.93	0.89
100	0.93	0.0123	74.84	76.14	75.97	0.92	0.94	0.93

## **Abstract**

The consequences from agricultural intensification are among the major threats for global biodiversity. As intensification follows an ongoing trend, species richness seems to face the already proclaimed sixth mass extinction at least in the near future. However, this extinction of species can occur immediately but also time-delayed, conceptualized extinction debt. While such time lags in semi-natural habitats have been researched extensively so far, empirical evidence on extinction debt of agrobiodiversity is rare. Here, we provide such an analysis of Austrian agroecosystems by relating current species richness of several taxonomic groups with land-use information of the second half of the 20<sup>th</sup> century gained through our calculations incorporating detailed habitat maps and a key socioeconomic land-use indicator (human appropriation of net primary production, HANPP). Our results suggest that species-richness patterns reflect a legacy of only about two decades for perennial vascular plants (22 years) and butterflies (18 years). These relative short time lags of agrobiodiversity, compared to semi-natural habitat specialists, underline that future intensification of agroecosystems will have rather immediate effects on biodiversity. Conservational as well as land-use policy measurements need to be chosen wisely as time for correcting detrimental impacts is limited.

## Zusammenfassung

Die Folgen landwirtschaftlicher Intensivierung zählen weltweit zu den größten Bedrohungen von Biodiversität. Da Intensivierung fortwährend zunimmt, wird die bereits ausgerufene sechste Massen Extinktion wohl spätestens in naher Zukunft eintreten. Wie auch immer, das Aussterben von Arten kann unmittelbar aber auch zeitverzögert auftreten, letzteres wird durch das Konzept „Extinction debt“ definiert. Während solche zeitlichen Verzögerungen in naturnahen Habitaten bereits ausführlich untersucht wurden, sind wenige Studien über Extinction debt von Agrar-Biodiversität zu finden. In dieser Arbeit präsentieren wir eine derartige Untersuchung von österreichischen Agrar-Ökosystemen, indem wir aktuellen Artenreichtum von verschiedenen taxonomischen Gruppen mit Landnutzungsinformationen in Relation setzen. Die Daten zur Landnutzung aus der zweiten Hälfte des 20. Jahrhunderts stammen aus unseren Berechnungen aus detaillierten Habitat-Karten und einem sozioökonomischen Landnutzungsindikator (Human Appropriation of Net Primary Production, HANPP). Unsere Ergebnisse legen nahe, dass in österreichischen Agrarlandschaften Biodiversität sich relativ rasch an Veränderungen von Landschaftsstruktur/Habitatausstattung anpassen kann: innerhalb von etwa zwei Jahrzehnten im Fall mehrjähriger Gefäßpflanzen (22 Jahre) und Schmetterlinge (18 Jahre); und möglicherweise sogar noch rascher im Fall einjähriger Pflanzen und Heuschrecken. Diese relativ kurzen zeitlichen Verzögerungen bei Agrar-Biodiversität, im Vergleich zu Spezialisten naturnaher Lebensräume zeigen, dass die zukünftige Intensivierung von Agrar-Ökosystemen ziemlich unmittelbare Effekte auf Biodiversität haben wird. Naturschutzfachliche sowie landnutzungspolitische Maßnahmen sollten gut überlegt sein, denn die Zeit um schädliche Auswirkungen auszubessern ist streng limitiert.

# Curriculum Vitae

## Personal details

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Name                    Johannes Paul GATTRINGER

## Education

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10/2011 – 02/2014      **Master studies:** Ecology (MSc)  
special emphasis: vegetation ecology, human ecology  
University of Vienna, Austria  
**Master thesis:** Land-use legacies on agrobiodiversity in Austria

10/2007 – 10/2011      **Bachelor studies:** Nutritional sciences (Bakk.rer.nat.)  
University of Vienna, Austria  
**Bachelor thesis:** Evening primrose *Oenothera spp.* in human nutrition

09/2001 – 06/2006      **College for tourism** - school leaving examination  
main area of training: tourism management  
Tourismusschulen Krems, Austria

## Language skills

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Mother tongue	German	
Other languages	English	proficient user
	French	independent user
	Italian	basic user

## Computer skills

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Operating systems	Windows, Mac OS X, Linux Ubuntu & Mint
Office software	Microsoft Office - Word, Excel, PowerPoint, Access OpenOffice, LibreOffice
Statistical software	R, SPSS, SigmaPlot, Statgraphics, Primer6
GIS	ESRI ArcGIS, Quantum GIS, Python
Design	LaTeX, GIMP, Adobe Photoshop, Adobe InDesign

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