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Potential of GLMM in modelling invasive spread: Supplement A

Literature analysis

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Literature search

Web of knowledge

Date of search: 12.07.2011

Database(s): all

Years: 2002–2011

Query: topic = (("mixed-effect\$" SAME model\$) OR "mixed model\$" OR GLMM\$) AND (invasi* OR "non-native\$" OR "non-indigenous" OR exotic\$ OR alien\$ OR weed*)

Results were refined by excluding non-english publications and by subject areas. Subject areas included in final search results were:

Agriculture	Forestry
Biodiversity & Conservation	Genetics & Heredity
Business & Economics	Geography
Developmental Biology	Marine & Freshwater Biology
Entomology	Mathematical & Computational Biology
Environmental Sciences & Ecology	Plant Sciences
Evolutionary Biology	Urban Studies
Fisheries	Zoology

Number of hits: 153

Scopus

Date of search: 07.07.2011

Database: Life Sciences

Years: 2002–2011

Query: article title|abstract|keywords = ("mixed-effect*" OR "mixed model*" OR GLMM*) AND (invasi* OR "non-native*" OR "non-indigenous" OR exotic* OR alien*)

Results were refined by excluding non-english publications and by subject areas. Subject areas included in final search results were:

Agricultural and Biological Sciences	Earth and Planetary Science
Biochemistry, Genetics and Molecular Biology	Environmental Science
Biology	

Number of hits: 73

Google Scholar

Date of search: 08.07.2011

Years: 2002–2011

Query: "with all of the words" = (mixed-effect OR GLMM) (invasion OR invasive OR non-native OR non-indigenous OR exotic OR alien); "without the words" = medicine medical surgery dermatology rheumatology optics psychology radiology pediatrics obstetrics neurology gastroenterology hepatology endocrinology pathology hematology cardiovascular cardiology immunology anesthesiology urology veterinary

Number of hits: 958

Search results were read with Zotero 2.1.8 and exported to BibTex format. Using JabRef 2.6 duplicates, entries without journal names, non-english articles, dissertations, non-article publications, "grey literature", non-peer reviewed articles and articles obviously not dealing with invasion biology were discarded manually. Due to the large number of remaining papers and obviously high proportion of papers that did not treat invasion biology, we identified suitable articles using dynamic grouping in JabRef. For this purpose, we used the following query: title = invasi OR exotic OR alien OR non-?native OR non-?indigenous OR weed OR spread OR coloni OR introduced. The number of remaining papers was 101.

Literature review

The results of the searches in WOS, Scopus and Google Scholar were combined in a single BibTex database and duplicates were removed. The suitability of the remaining 133 articles, i.e. if they reported applications of GLMM in the field of invasion biology, was examined based on abstracts and, if necessary, the main text. Altogether, 116 articles proved to be suitable of which 50 were randomly chosen for further analysis.

The suitable articles were evaluated for several characteristics related to the GLMM analyses, such as type of dependent variable (metric, count, proportion, binary ...), distribution chosen for modelling (gaussian, Poisson, binomial ...), methods for estimating parameters and inference etc. The results of this literature review are presented below.

Results of literature review

Overview

In total, our literature searches found 116 papers reporting applications of GLMM in invasion biology. We analysed a random sample of 50 papers (out of 116) in which 97 GLMM setups were reported. Many of these setups were applied to several different, but statistically similar dependent variables, e.g. the same setup was used to model cover percentages of many different species in separate models, so that the 97 model setups accounted for a total of 526 models.

Types of studies applying GLMM in invasion biology

In the following, we describe the applications of GLMM in invasion biology based on the 97 model setups found in the random sample of 50 papers mentioned above.

The majority of GLMM setups was used in observational studies, but also experimental approaches occurred frequently (Fig. SA1). In most cases, the aim of study was to test the significance of relationships between dependent and independent variables. Markedly fewer studies focused on estimation of parameters for making predictions. Particularly, variation in random variables was rarely of interest (Fig. SA2) and, correspondingly, most papers did not even report variances or standard deviations of random effects.

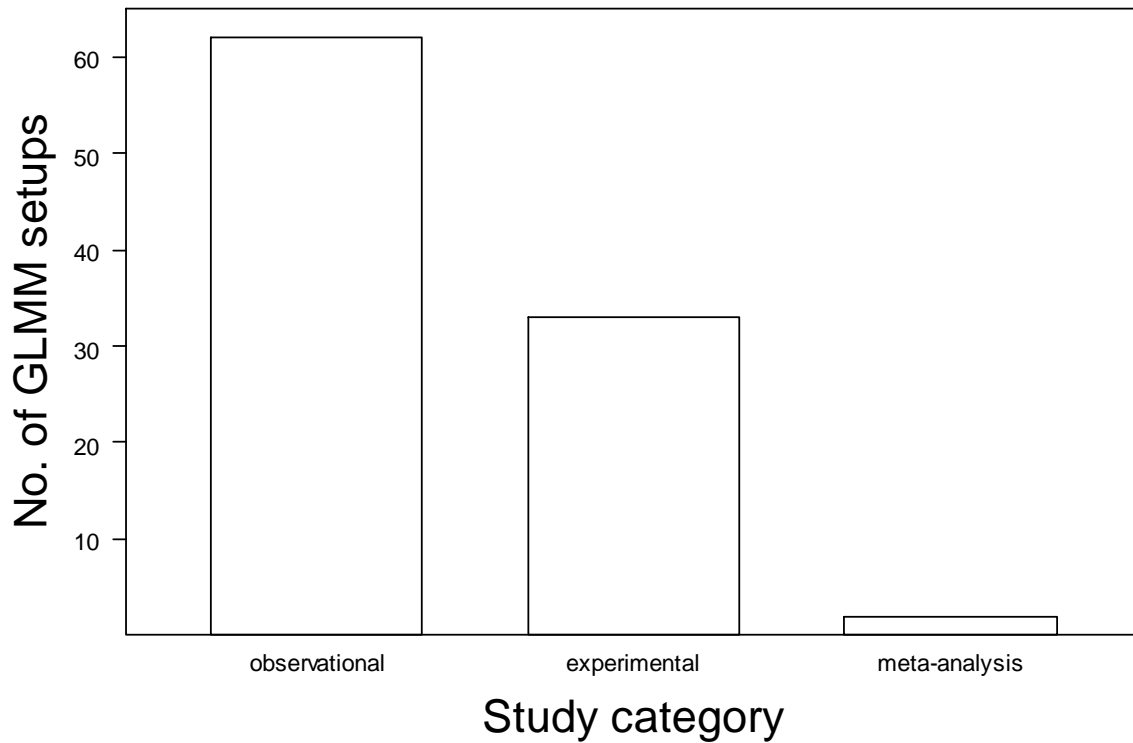


Fig. SA1 Frequencies of study categories: *observational*, non-manipulative field studies; *experimental*, manipulative experiments in the field, common garden or green house; *meta-analysis*, analysis of effect sizes from recent papers.

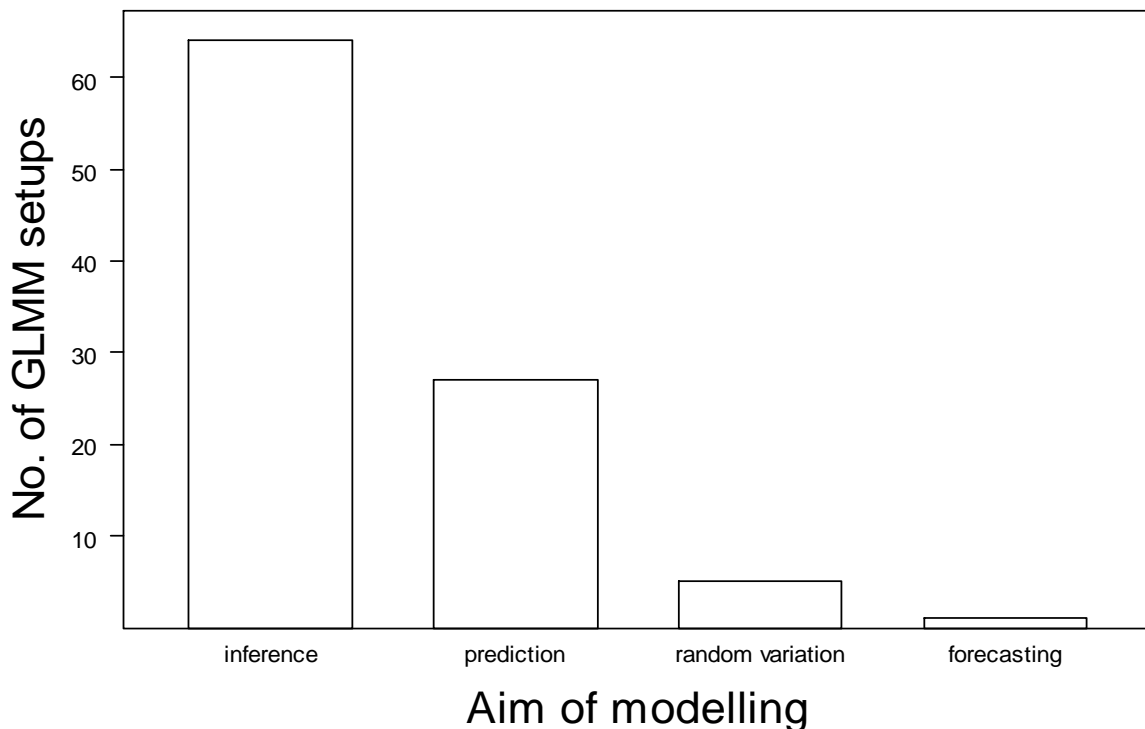


Fig. SA2 Frequencies of modelling aims: *inference*, only significance tests of relationships between dependent and predictor variables were desired; *prediction*, parameter estimates of fixed effects for calculating expected local (group) means was focused on (as a rule significance testing was important in these studies, too); *random variation*, parameters estimates of random effects, i.e. variances or standard deviations, were relevant or even most important; *forecasting*, calculation of expected values using model estimates on a new (larger) data set was the aim (only one study forecasting the distribution of a species in GIS grid cells).

Invasion biology comprises a plethora of ecological topics and so do applications of GLMM. Classical topics, i.e. invasiveness, invasibility and evolution (or selection) of invasive genotypes, accounted for roughly 40 % of model setups. More general aspects of population ecology of non-native species were treated frequently, and surprisingly many studies addressed impacts of non-native species on native species, communities or ecosystems, whereas dispersal and management of non-native species was studied rather rarely with GLMM (Fig. SA3).

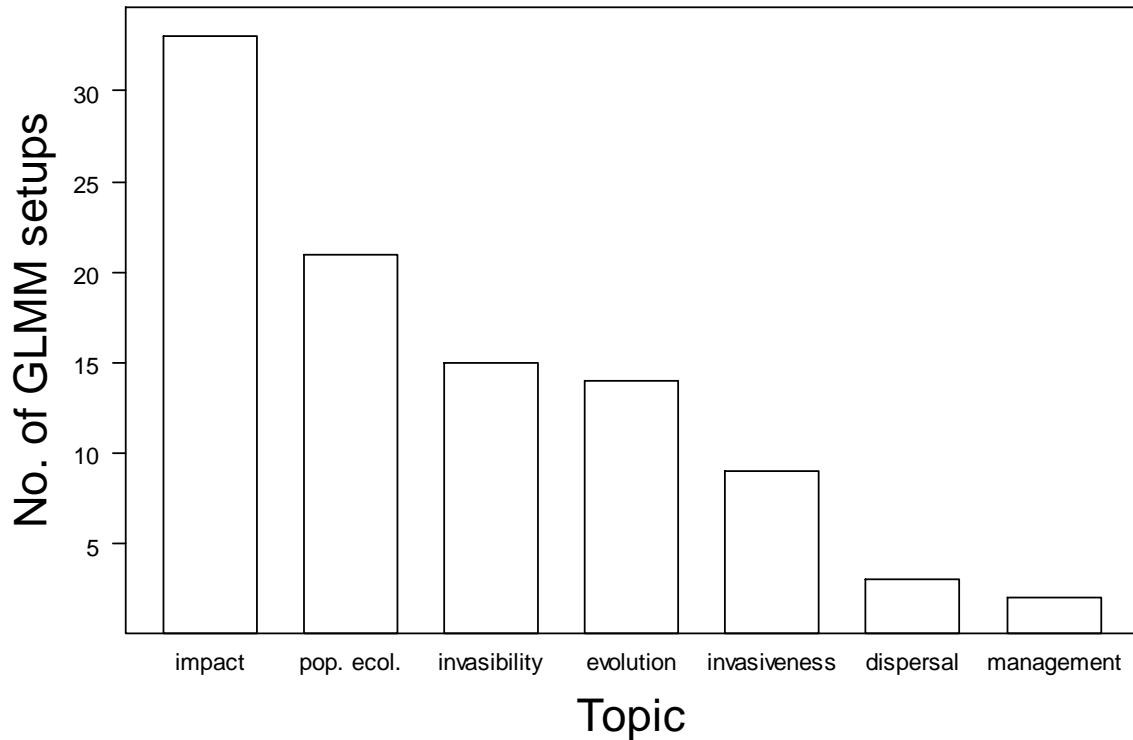


Fig. SA3 Frequencies of scientific topics: *impact*, model setups using invader abundance (in a broad sense) as predictor variable and native species, communities or ecosystem properties as response; *pop. ecol.*, population ecology of non-native species; *invasibility*, model setups using habitat or community properties as predictor variables and a measure of invasion success as response; *evolution*, comparisons of genotypes or phenotypes among native and invaded ranges or among habitats; *invasiveness*, model setups using traits of non-native species as predictor variables and a measure of invasion success as response; *dispersal*, studies of propagule pressure of non-native species; *management*, management of population densities of non-native species.

Variables and distributions

The most common dependent variables of GLMM setups were phenotypic traits, abundances of animal or plant individuals, and species richness, followed by population parameters, such as demographic rates, properties of communities or ecosystems and invasion success (Fig. SA4).

In the majority of setups, the dependent variables were counts, which corresponds to frequent use of abundances, species richness, and countable phenotypic plant traits, such as number of flowers or seeds (Fig. SA5). Almost a quarter of model setups used continuous dependent variables, which most often were phenotypic measurements, such as biomass, heights or widths, but also community or ecosystem properties, e.g. diversity measures. Further, a large part of dependent variables represented binomial outcomes. Among these, proportions, such as cover percentages and rates of survival, germination etc., were somewhat more common, than binary variables (presence-absence, invasion success, mortality etc.).

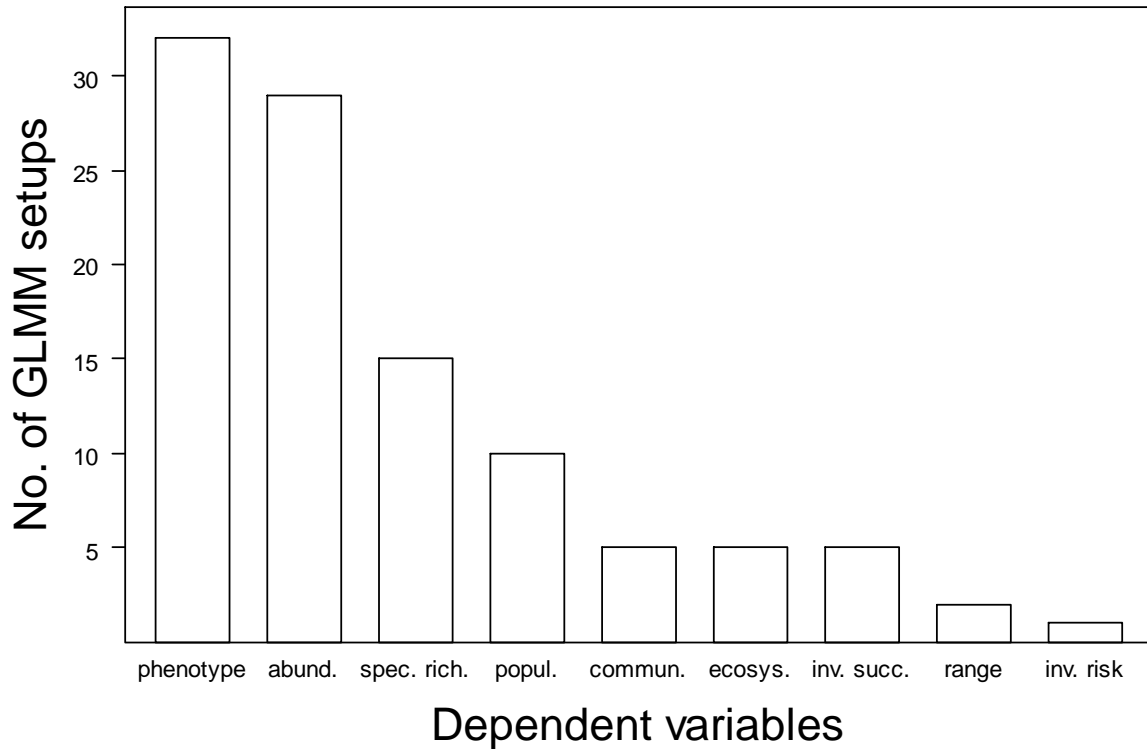


Fig. SA4 Frequencies of thematically grouped dependent variables. Abbreviations: *abund.*, abundance; *spec. rich.*, species richness; *popul.*, population properties; *commun.*, community properties; *ecosys.*, ecosystem properties; *inv. succ.*, invasion success; *inv. risk*, invasion risk.

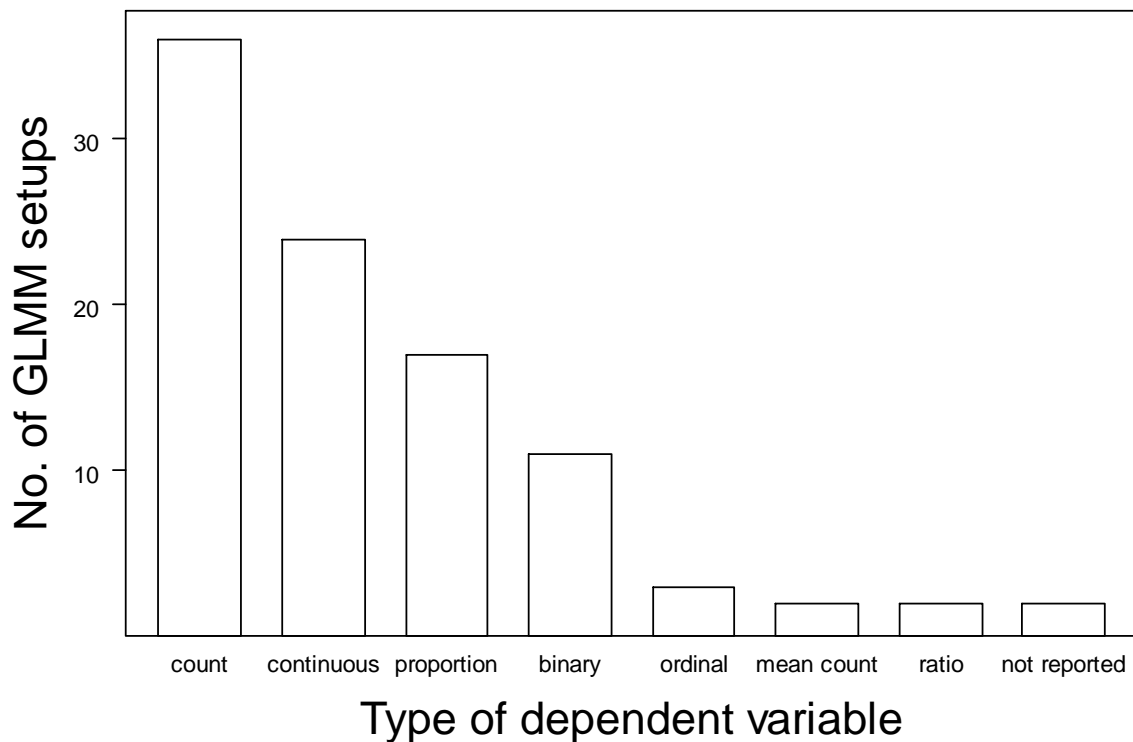


Fig. SA5 Frequencies of types of dependent variables.

The choice of distribution in the GLMM (Fig. SA6) did not fully reflect the pattern of dependent variable types described above. Gaussian (i.e. normal) distribution was applied in 45 % of all cases, while continuous variables (incl. mean counts and ratios) made up only 29 %. Although counts with large means and proportions may be

satisfactorily modeled with Gaussian distribution in some cases, these results suggest that binomial distribution (29 % of variables vs. 19 % of model distributions) and Poisson distribution (37 % of variables vs. 18% of model distributions, the latter including negative binomial distribution) are still not sufficiently used.

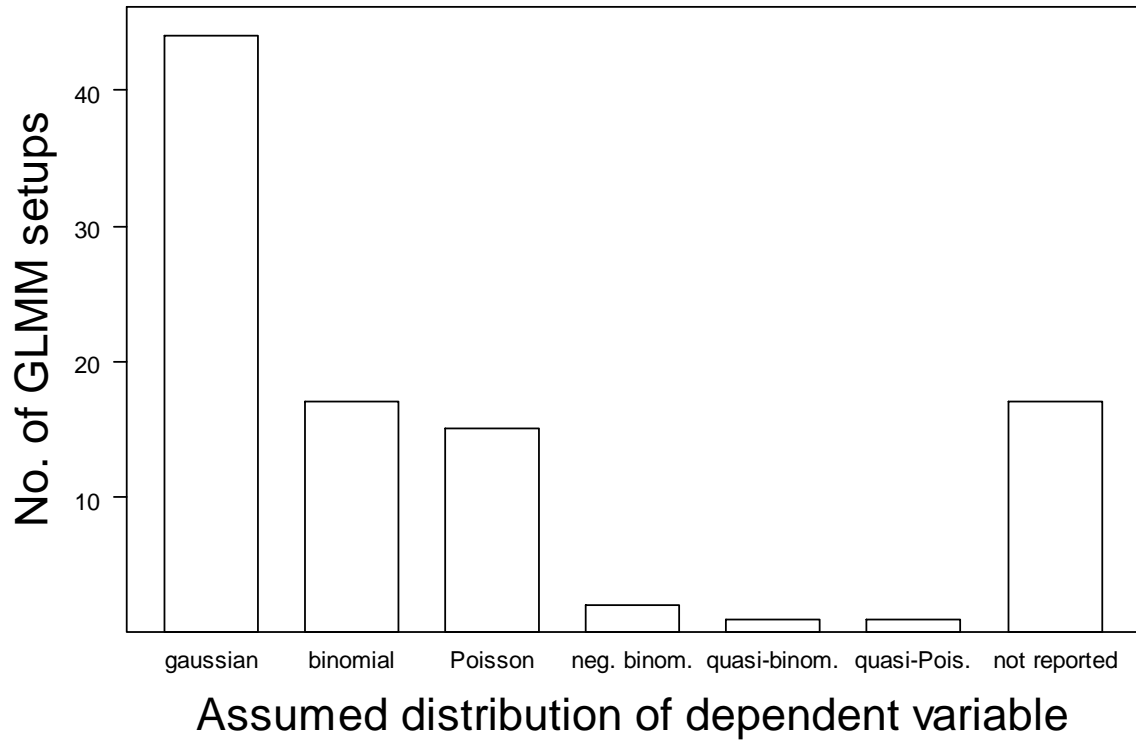


Fig. SA6 Statistical distribution of dependent variables assumed in GLMM. Abbreviations: *neg. binomial*, negative binomial; *quasi-binom.*, quasi-binomial; *quasi-Pois.*, quasi-Poisson.

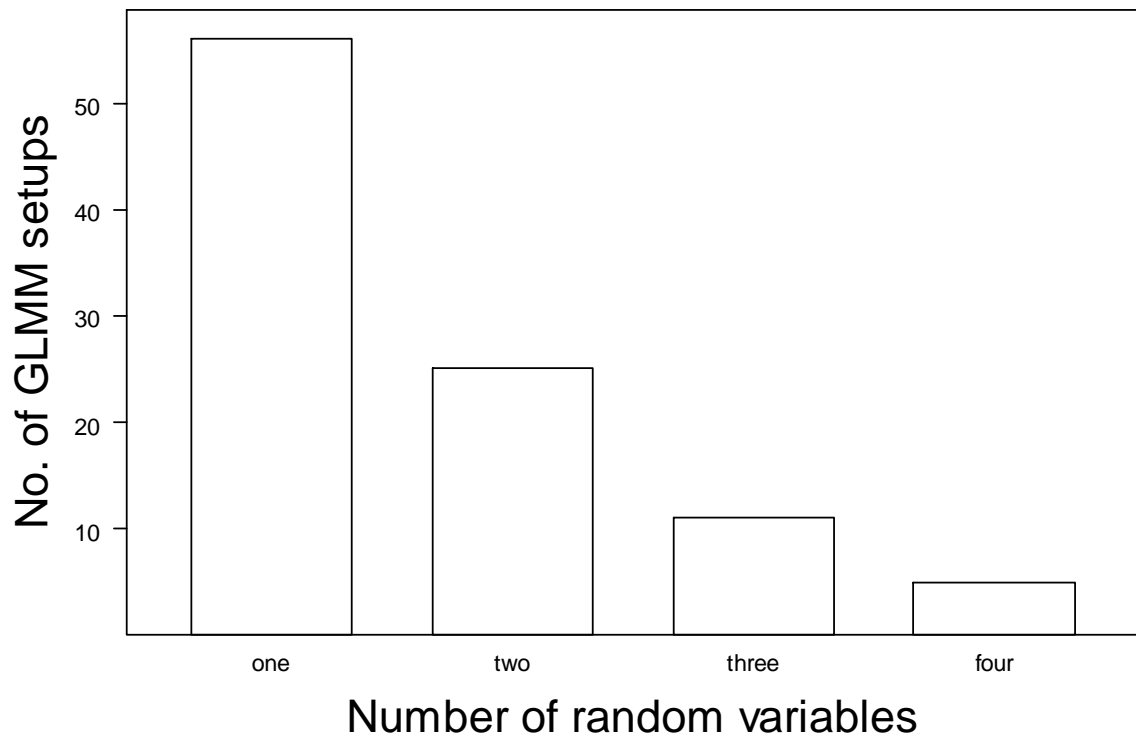


Fig. SA7 Frequencies of the numbers of random grouping variables included in GLMM.

Most often studies dealt with a single random variable, but up to four different levels of random grouping variables were included in GLMM (Fig. SA7). If multiple random variables occurred, these were most often (74 %) nested grouping variables (e.g. plots nested in blocks, or sites nested in regions), while crossed random variables were much less common (14 %). For the remaining 12 % the design of multiple random variables (crossed or nested) was not reported.

In by far the most cases (92 %), random variables were only included in the model to obtain valid p-values and estimates for fixed effects. Typically, these "nuisance variables" were due to experimental design (transects, blocks, plots), geographical location (regions, sites) or sampling of multiple populations, but also taxonomic units were used quite frequently (Fig. SA8).

A third of GLMM setups analysed time series of data collected repeatedly from the same individuals or plots etc. Most of these studies accounted for non-independence of repeated observations by including a random effect (intercept) of the respective grouping variable, e.g. 'individual' or 'plot'. Some studies also accounted for variation among time periods (Fig. SA8), e.g. among years. However, only 15 % of setups modelling temporally auto-correlated data included specifications of appropriate correlation structures.

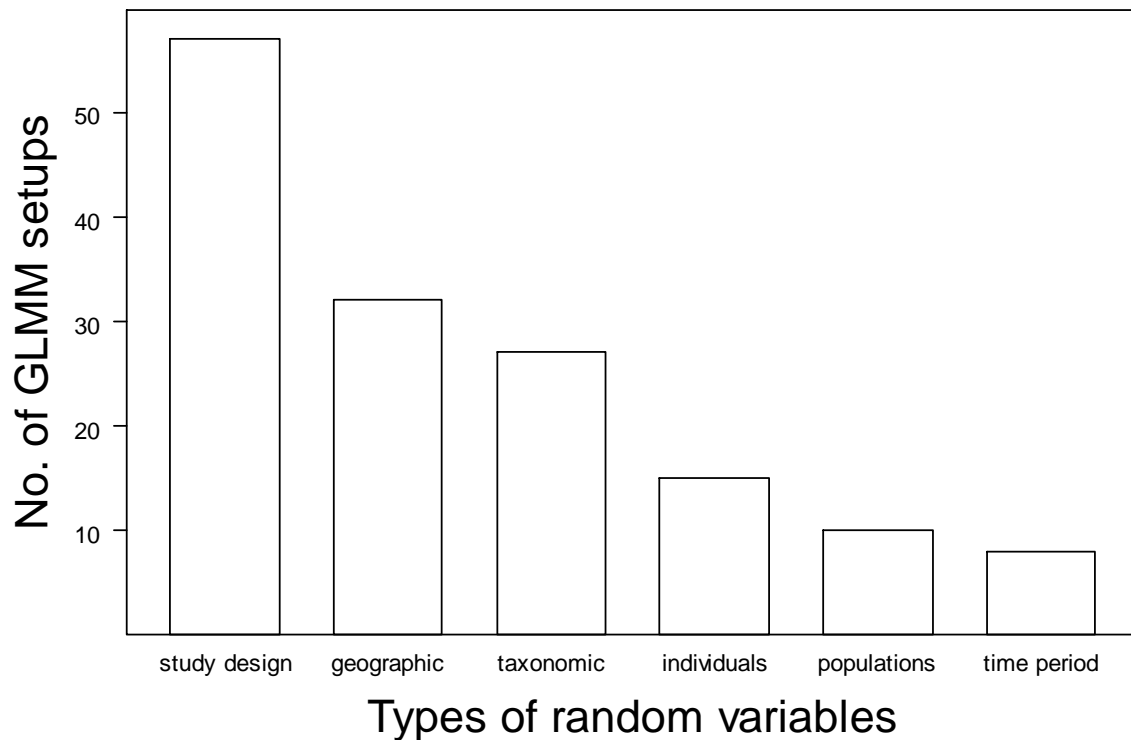


Fig. SA8 Frequencies of types of random variables included in GLMM. Total count of types of random variables (151) was larger than the number of model setups (97) because of multiple random effects in some of the model setups. Two singular categories are omitted ('ecological guild' and 'study' in a meta-analysis).

Statistical packages

The most popular statistical package was R (67 %). Among those studies that reported the particular R library, 'lme4', 'glmmPQL' and 'nlme' were common. The second most popular statistical package was SAS (13 %) with the procedures 'GLIMMIX', 'MIXED' and 'NLMIXED'. Other software was apparently less common, but a considerable number of studies did not report which software was used (Fig. SA9).

Which model building strategies are used?

Explorative model building was not very common among the analysed GLMM setups. In about two third of cases, the fixed effects structure was predetermined by experimental design or by hypothesis (Fig. SA10). Regarding random effects, the rate of setups engaging in model building was as low as 7 %, reflecting the fact that random variables most often were nuisance variables (Fig. SA11).

Flaws in GLMM applications in invasion biology

- Using Penalized Quasi-Likelihood (PQL) with large standard deviations (SD) of random effects: 11 studies reported use of PQL; out of these 1 had large SD, the others did not report the magnitude of SD.
- Using PQL with binary variables or with binomial with less than 5 successes and failures: 17 setups used binomial distribution; of these, 11 modeled binary outcomes (4 used PQL, 3 did not, 4 did not report the method of estimation) and 6 modeled proportion data (1 setup modeled a dependent variable with less than 5 successes and failures using PQL, the other five modeled > 5 successes and failures).
- Using PQL with Poisson distribution and mean counts less than 5: 15 setups used Poisson distribution; of these, 4 modeled means (partly) less than 5; of these four, 1 used PQL, 1 used Gauss-Hermite quadrature and 2 did not report the estimation method.
- Using random effects with less than 4 levels: 21 setups did, 69 did not, 6 did not report the number of levels.
- Using Wald tests with standard “between-within” calculation of degrees of freedom (DF) where Satterthwaite or Kenward-Roger correction would have been recommended: many studies did not report explicitly, if they used Wald tests; apparently Wald test were used quite frequently, but corrections of DF were reported very rarely; thus, it seems that this mistakes occurs regularly.

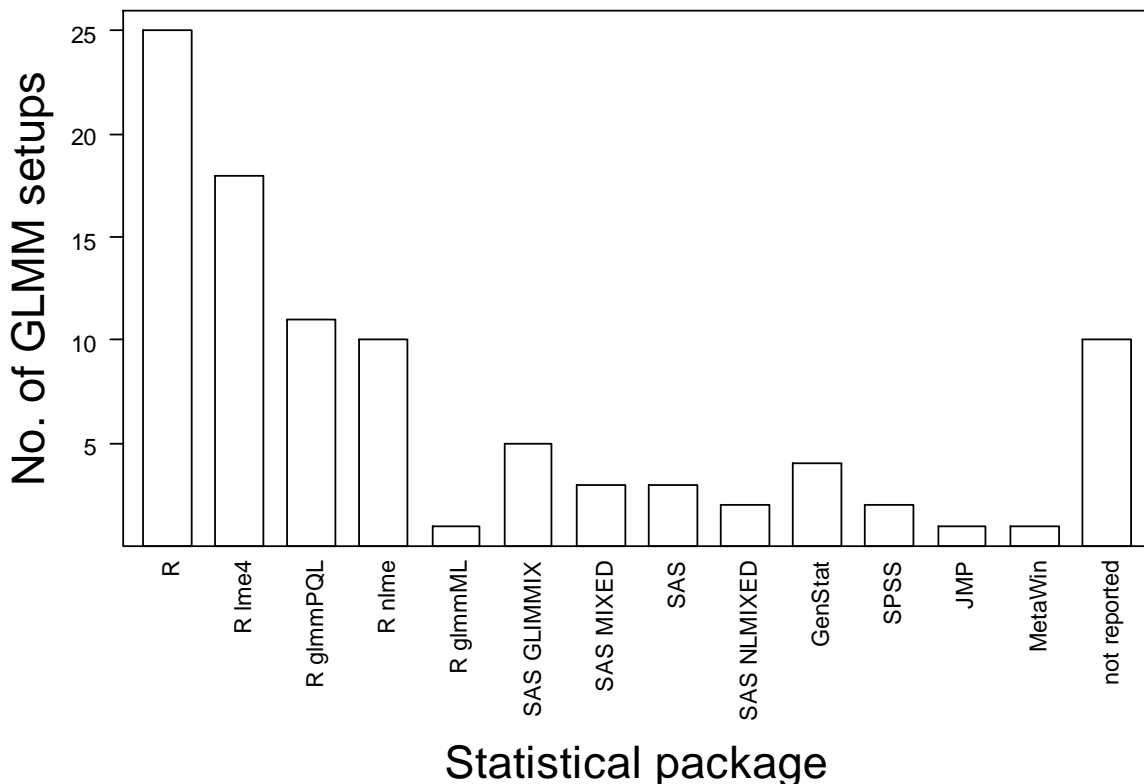


Fig. SA9 Frequencies of statistical software packages used for GLMM.

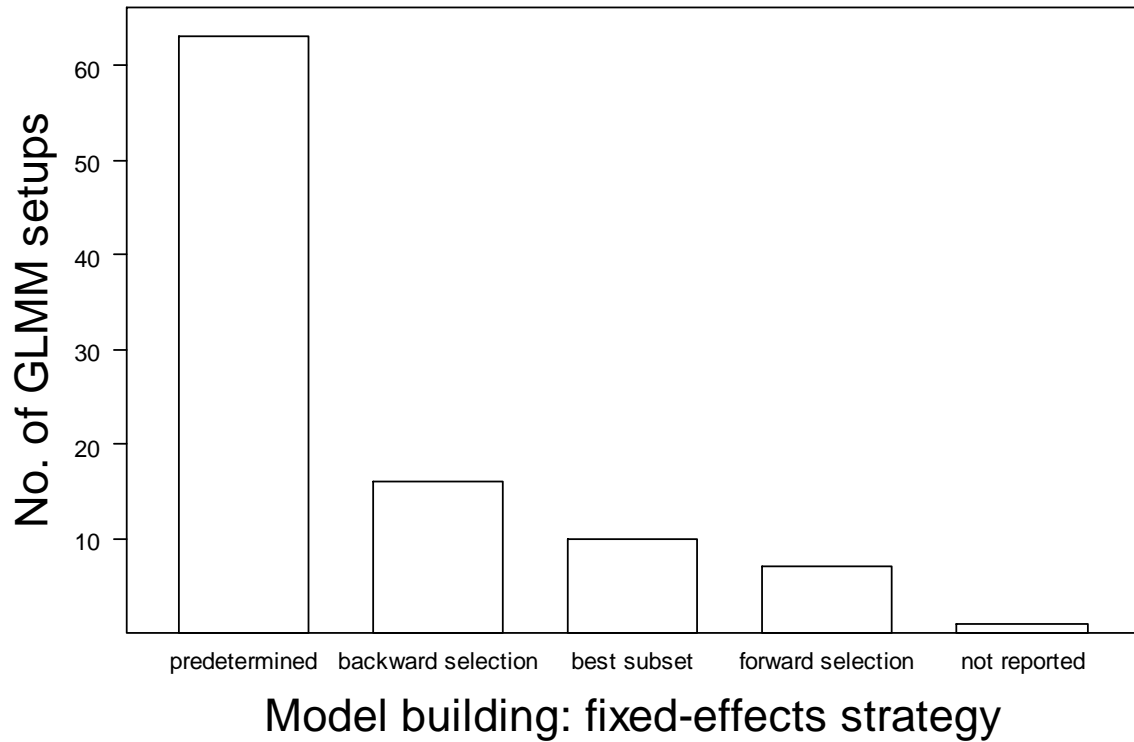


Fig. SA10 Frequencies of model building strategies for fixed effects.

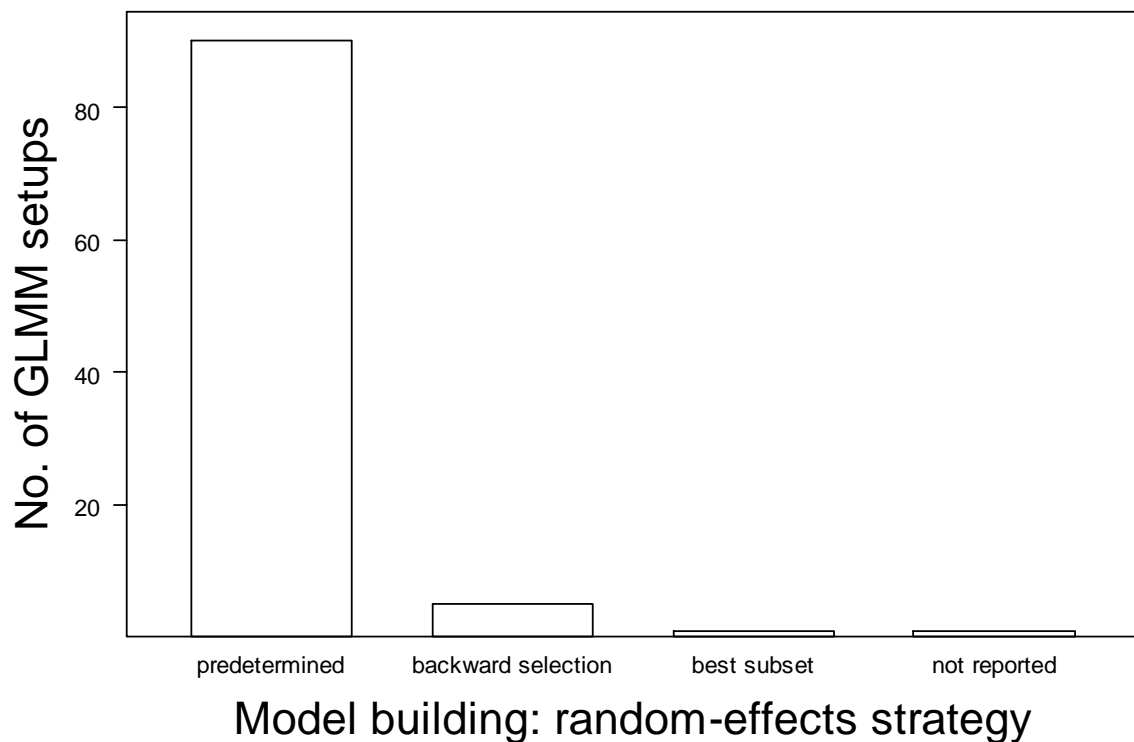


Fig. SA11 Frequencies of model building strategies for random effects.

Articles used in literature analysis

The following list contains the 116 articles reporting GLMM applications in invasion biology that were found in the literature searches documented in ch. 1 (this

Supplement). The articles were sorted after ascending random numbers. The first 50 articles were included in the literature analysis.

1. Masaka, Kazuhiko; Yamada, Kenji; Koyama, Yasuhiro; Sato, Hajime; Kon, Hirokazu & Torita, Hiroyuki; Changes in size of soil seed bank in *Robinia pseudoacacia* L. (Leguminosae), an exotic tall tree species in Japan: Impacts of stand growth and apicultural utilization; *Forest Ecology and Management*; 260; 5; 780–786; 2010
2. Hazelton, P. D. & Grossman, G. D.; The effects of turbidity and an invasive species on foraging success of rosyside dace (*Clinostomus funduloides*); *Freshwater Biology*; 54; 9; 1977–1989; 2009
3. Bartomeus, I. & Vilà, M.; Breeding system and pollen limitation in two supergeneralist alien plants invading Mediterranean shrublands; *Australian Journal of Botany*; 57; 2; 109–115; 2009
4. Elias, S. P.; Lubelczyk, C. B.; Rand, P. W.; Lacombe, E. H.; Holman, M. S. & Smith, R. P.; Deer browse resistant exotic-invasive understory: An indicator of elevated human risk of exposure to *Ixodes scapularis* (Acari : Ixodidae) in southern coastal Maine woodlands; *Journal of Medical Entomology*; 43; 6; 1142–1152; 2006
5. Schlick-Steiner, B. C.; Steiner, F. M. & Pautasso, M.; Ants and people: a test of two mechanisms potentially responsible for the large-scale human population-biodiversity correlation for Formicidae in Europe; *Journal of Biogeography*; 35; 12; 2195–2206; 2008
6. Moron, D.; Lenda, M.; Skórka, P.; Szentgyörgyi, H.; Settele, J. & Woyciechowski, M.; Wild pollinator communities are negatively affected by invasion of alien goldenrods in grassland landscapes; *Biological Conservation*; 142; 7; 1322–1332; 2009
7. Chun, Y. J. and Kim, C. G. and Moloney, K. A.; Comparison of life history traits between invasive and native populations of purple loosestrife (*Lythrum salicaria*) using nonlinear mixed effects mode; *Aquatic Botany*; 93; 4; 221–226; 2010
8. Reiter, M. E. & Lapointe, D. A.; Landscape factors influencing the spatial distribution and abundance of mosquito vector *Culex quinquefasciatus* (Diptera : Culicidae) in a mixed residential-agricultural community in Hawai'i; *Journal of Medical Entomology*; 44; 5; 861–868; 2007
9. Nagamitsu, T.; Yamagishi, H.; Kenta, T.; Inari, N. & Kato, E.; Competitive effects of the exotic *Bombus terrestris* on native bumble bees revealed by a field removal experiment; *Population Ecology*; 52; 1; 123–136; 2010
10. Gea-Izquierdo, G.; Gennet, S. & Bartolome, J. W.; Assessing plant-nutrient relationships in highly invaded Californian grasslands using non-normal probability distributions; *Applied Vegetation Science*; 10; 343–U37; 2007
11. Maurel, N.; Salmon, S.; Ponge, J. F.; Machon, N.; Moret, J. & Muratet, A.; Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands?; *Biological Invasions*; 12; 6; 1709–1719; 2010
12. Xu, C. Y.; Julien, M. H.; Fatemi, M.; Girod, C.; Van Klinken, R. D.; Gross, C. L. & Novak, S. J.; Phenotypic divergence during the invasion of *Phyla canescens* in Australia and France: evidence for selection-driven evolution; *Ecology Letters*; 13; 1; 32–44; 2010
13. Bartuszevige, A. M.; Hughes, M. R.; Bailer, A. J. & Gorchov, D. L.; Weather-related patterns of fruit abscission mask patterns of frugivory; *Canadian Journal of Botany-revue Canadienne De Botanique*; 84; 5; 869–875; 2006
14. Carvalheiro, L. G.; Buckley, Y. M. & Memmott, J.; Diet breadth influences how the impact of invasive plants is propagated through food webs; *Ecology*; 91; 4; 1063–1074; 2010
15. Scherber, C.; Mwangi, P. N.; Schmitz, M.; Scherer-Lorenzen, M.; Bessler, H.; Engels, C.; Eisenhauer, N.; Migunova, V. D.; Scheu, S.; Weisser, W. W.; Schulze, E. D. & Schmid, B.; Biodiversity and belowground interactions mediate community invasion resistance against a tall herb invader; *Journal of Plant Ecology-uk*; 3; 2; 99–108; 2010
16. Kark, S. & Sol, D.; Establishment success across convergent Mediterranean ecosystems: an analysis of bird introductions; *Conservation Biology*; 19; 5; 1519–1527; 2005
17. Cheng, Y. W. & LeClair, L. L.; A quantitative evaluation of the effect of freezing temperatures on the survival of New Zealand mudsnails (*Potamopyrgus antipodarum* Gray, 1843), in Olympia Washington's Capitol Lake; *Aquatic Invasions*; 6; 1; 47–54; 2011
18. Gómez-González, S., Torres-Díaz C., Valencia G., Torres-Morales P., Cavieres L.A. & Pausas J.G.; Anthropogenic fires increase alien and native annual species in the Chilean coastal matorral; *Diversity and Distributions*; 17; 1; 58–67; 2011
19. Thiele, J.; Isermann, M.; Otte, A. & Kollmann, J.; Competitive displacement or biotic resistance? Disentangling relationships between community diversity and invasion success of tall herbs and shrubs; *Journal of Vegetation Science*; 21; 2; 213–220; 2010
20. Alexander, J. M.; Genetic differences in the elevational limits of native and introduced *Lactuca serriola* populations; *Journal of Biogeography*; 37; 10; 1951–1961; 2010

21. Swei, A.; Ostfeld, R. S.; Lane, R. S. & Briggs, C. J.; Effects of an invasive forest pathogen on abundance of ticks and their vertebrate hosts in a California Lyme disease focus; *Oecologia*; 166:91–100; 2010
22. Dohzono, I.; Kunitake, Y. K.; Yokoyama, J. & Goka, K.; Alien bumble bee affects native plant reproduction through interactions with native bumble bees; *Ecology*; 89; 11:3082–3092; 2008
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26. Bertheau, C.; Brockerhoff, E. G.; Roux-Morabito, G.; Lieutier, F. & Jactel, H.; Novel insect-tree associations resulting from accidental and intentional biological ‘invasions’: a meta-analysis of effects on insect fitness; *Ecology letters*; 13; 4:506–515; 2010
27. Engeman, R. M.; Groninger, N. P. & Vice, D. S.; A general model for predicting brown tree snake capture rates; *Environmetrics*; 14; 3:295–305; 2003
28. Monty, A. & Mahy, G.; Evolution of dispersal traits along an invasion route in the wind-dispersed *Senecio inaequidens* (Asteraceae); *Oikos*; 119:1563–1570; 2010
29. Pons, P.; Bas, J. M. & Estany-Tigerstrom, D.; Coping with invasive alien species: the Argentine ant and the insectivorous bird assemblage of Mediterranean oak forests; *Biodiversity and Conservation*; 19; 6:1711–1723; 2010
30. Buckley, Y. M.; Briese, D. T. & Rees, M.; Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set; *Journal of Applied Ecology*; 40; 3:481–493; 2003
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