

## Review

## Addressing context dependence in ecology

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**Context dependence is widely invoked to explain disparate results in ecology. It arises when the magnitude or sign of a relationship varies due to the conditions under which it is observed. Such variation, especially when unexplained, can lead to spurious or seemingly contradictory conclusions, which can limit understanding and our ability to transfer findings across studies, space, and time. Using examples from biological invasions, we identify two types of context dependence resulting from four sources: mechanistic context dependence arises from interaction effects; and apparent context dependence can arise from the presence of confounding factors, problems of statistical inference, and methodological differences among studies. Addressing context dependence is a critical challenge in ecology, essential for increased understanding and prediction.**

### The prevalence and problem of context dependence

Ecological studies examining the same question or process often reach different conclusions. In invasion ecology, for example, studies have found that the phylogenetic relatedness of alien to native species can inhibit or facilitate invasion [1,2], the relationship between native and alien species richness can vary from positive to negative [3,4], and the effect of disturbance on invasion is equivocal and inconsistent [5,6]. When studies addressing the same question reach different conclusions, the different outcomes are often attributed to **context dependence** (see [Glossary](#)). Context dependence, or contingency, refers to situations where relationships vary depending on the conditions – the context – under which they are observed ([Figure 1](#)) [7–10]. It includes situations where the magnitude (strength) or sign (direction) of a relationship differs under different biotic, abiotic, spatiotemporal, or observational circumstances ([Figure 1](#) and [Box 1](#)).

Context dependence is commonly and increasingly invoked in ecology (Appendix S1, Figure S1, and Table S1 in the supplemental information online) [11–17], as well as in other fields typified by high complexity, large scales, and heavy reliance on observational studies, such as conservation biology [18,19], evolutionary biology [20,21], and epidemiology [22,23]. Context dependence provides a convenient shorthand to describe variation within and between (potentially myriad) studies and is reported across all study types [24–28]. However, because context dependence can result from many processes (as discussed below), unless the underlying causes are identified, concluding that outcomes are context dependent provides little insight by itself. Furthermore, because ‘context dependence’ is often used to describe disparate findings, widespread use of the term could suggest that there are few general principles in ecology, that ecological relationships are largely unpredictable, and that ecological phenomena can only be understood on a case-by-case basis [29,30]. Here we argue that researchers can gain greater insight into ecological processes if they recognise the different sources of context dependence and account for them in the design, interpretation, and communication of their studies.

We define context dependence and propose a novel typology based on two types and four sources of context dependence ([Figure 2](#)). We illustrate our typology using examples from

### Highlights

‘Context dependence’ is widely used to describe disparate results in ecology, but the term is poorly defined and inconsistently used.

Context dependence arises when ecological relationships vary in magnitude or sign, depending on the conditions under which they are observed.

Context dependence can result from multiple factors and processes, so, unless the underlying causes are identified, concluding that relationships are context dependent provides limited understanding.

We distinguish between apparent and mechanistic context dependence, with the former an artefact of study design and approach and the latter reflecting ecological interaction effects.

Recognising and addressing the different sources of context dependence should facilitate increased understanding, prediction, and generalisation in ecology.

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biological invasions, a field where context dependence is prominent and widely discussed (Box 1, Figure S2 and Table S2), but we propose that the typology is applicable across all areas of ecology. We outline steps for addressing the different types and sources of context dependence (Figure 3). By understanding ways in which context dependence can arise, ecologists should be better placed to distinguish fundamental (mechanistic) from **apparent context dependence**, increasing predictive understanding in ecology.

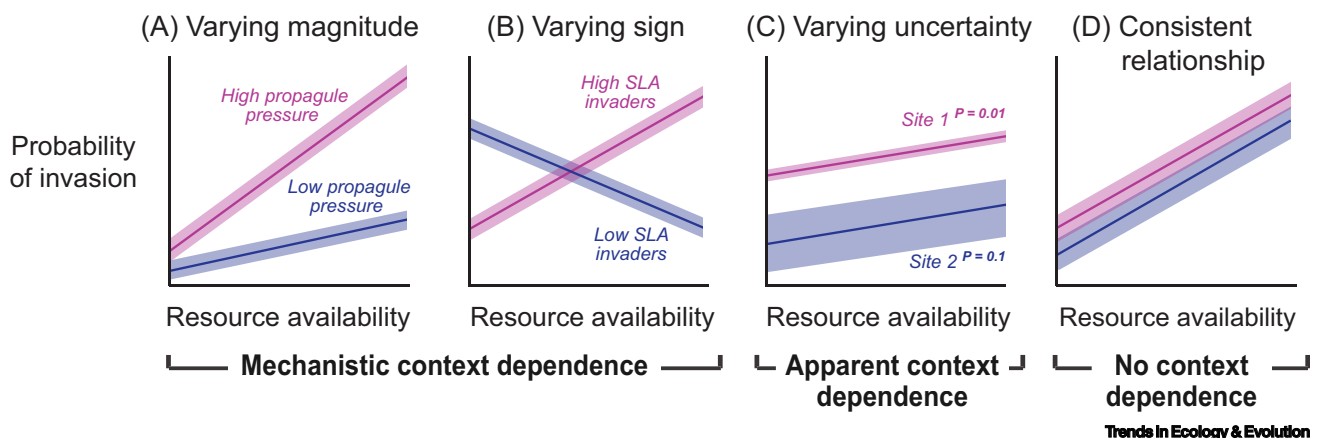
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### A typology of context dependence

We identify two types of context dependence resulting from four sources (Figure 2 and Table S3). **Mechanistic context dependence** occurs when a relationship, say between variables **X** and **Y**, fundamentally differs under different ecological and spatiotemporal conditions. Such relationships arise from (i) **interaction effects** of another variable, **Z**, which modifies the effect of **X** on **Y**, reflecting ecological processes. Apparent context dependence occurs when the relationship between variables **X** and **Y** does not differ but appears to due to: (ii) the presence of **confounding factors** that are either unaccounted for or are measured and accounted for in some studies but not others; (iii) problems of **statistical inference** where studies differ in sampling accuracy and precision, **statistical power**, or interpretation of statistical measures; and (iv) **methodological differences** among studies whereby studies observe and measure variables or relationships in different ways. The four sources of context dependence can co-occur and manifest in various ways (Figure 1). When individual studies use consistent methods, accurate approaches, and comparable study designs, within-study variation should be driven largely by interacting or confounding factors, whereas variation among studies can also reflect issues related to statistical inference or differences in study methodology.

Type: mechanistic; source: (i) interaction effects

'Interaction effects' (or interaction modifications [31] or effect modifications [22]) refers to higher-order interactions between three or more factors (**X**, **Y**, and **Z**). Interaction effects can result in relationships between **X** and **Y** being magnified, reduced, or reversed as **Z** values vary [11,32]. In Australia, for



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Figure 1. Context dependence may be invoked when the observed relationship between two variables varies in (A) magnitude (strength), (B) sign (direction), and (C) uncertainty, applied here to hypothetical examples from plant invasions. However, there is only evidence of real (mechanistic) context dependence in (A) and (B) and not in (C) [or (D)], because relationships in (C) do not vary in magnitude or sign, just statistical significance, as represented by hypothetical *P* values; (C) shows an example that could lead to apparent context dependence between Sites 1 and 2 if there are issues with statistical inference (see Figure 2 and main text). (D) Both cases show the same relationship (no context dependence). Forms of context dependence are not mutually exclusive and can co-occur. In this illustrative schematic, the independent variable **X** is resource availability, and the dependent **Y** variable is the probability of invasion: (A) magnitude of relationship depends on propagule pressure (context = propagule pressure); (B) sign of relationship depends on invader traits (high or low specific leaf area, SLA) (context = invader SLA); (C) slopes of relationships in Sites 1 and 2 are identical, but differences in uncertainty and statistical power mean that the relationship could be viewed as statistically significant in Site 1 (*P* = 0.01) but not Site 2 (*P* = 0.1), such that the relationship could be misinterpreted as being context dependent (context = site).

example, the relationship between **invasive** fox (*Vulpes vulpes*) abundance and impact on native animals depends on the local abundance of dingoes (*Canis familiaris*), the apex predator, because dingoes suppress fox activity [33,34]. Interaction effects such as these can extend beyond two-way interactions and involve multiple interacting factors [19,22,35].

Context dependence arising from interaction effects reflects underlying causal relationships and should thus be consistent with, or can inform, theory (Box 2) [10]. For example, in a grassland experiment, the relationship between abundance of invading plant species and community diversity was consistent with theories of plant resource economics and competition [36,37]: invaders with resource-acquisitive strategies were more abundant in low-diversity communities, whereas the opposite was true in high-diversity communities [24]. Observed fine-scale variation in occupancy of giant bamboo (*Phyllostachys bambusoides*) in Japan corresponds with the stress gradient hypothesis [38] and reflects bamboo ecology and ecophysiology (see Figure IA in Box 1) [26]. And the fox–dingo example noted above is consistent with the mesopredator release hypothesis [39]. If important interaction effects are overlooked, observed relationships can appear uncertain within studies and can differ among studies.

Type: apparent; source: (ii) confounding factors

Confounding occurs when two or more independent variables, X and C, are correlated such that their effects on dependent variable Y cannot be disentangled [40,41]. Confounders can be considered ‘nuisance’ variables and can generate apparent context dependence because, unless their effects are eliminated or taken into account, they can exaggerate, suppress, reverse, or alter the manifestation of the **X–Y relationship** [18,22,41,42], especially when the relationship is weak [43]. For example, an apparent negative relationship between bullfrog (*Rana catesbeiana*) invasion and native frog species richness in eastern China disappears once the confounding effect of frog hunting by humans is considered (see Figure IB in Box 1) [44]. Similarly, without accounting for confounding variables, buckthorn (*Rhamnus cathartica*) invasion can appear to increase soil pH and leaf litter calcium flux in US forests [45]. Confounding can be especially problematic in observational studies (where independent variables and unidentified legacy effects can be less readily controlled than in experiments), in studies spanning a wide range of conditions, and in meta-syntheses (because confounding can affect findings at the synthesis level as well as findings of component studies) [18,22,41].

Type: apparent; source: (iii) statistical inference

Apparent context dependence can arise when studies estimating an X–Y relationship reach the wrong conclusion because measurements of X and Y are noisy, the effect of X on Y is weak, multiple comparisons are made and sample sizes are small, or statistical results are interpreted incorrectly [46–48]. Indeed, if studies rely on binary notions of statistical significance to judge the presence, magnitude, and sign of relationships, then, when statistical power is low – as is often the case in ecology [49] – studies will often find ‘statistically significant’ results that exaggerate the effect of X on Y or conclude that it goes in the wrong direction [46]. Such errors in the estimated magnitude or sign of relationships (**Type M error** and **Type S error**, respectively [46]) can be stochastic, leading to different studies reaching different conclusions mostly by chance alone [49]. The practice of categorising effects as significant or non-significant using *P* values or confidence intervals can also lead to apparent context dependence due to differences in the statistical power of studies [48,50]. This is compounded by errors in interpretation and questionable research practices, which are common in ecology and related fields [51,52]. For example, Fidler *et al.* [52] found that 63% of 67 conservation biology papers that used null hypothesis significance testing misinterpreted statistical non-significance as evidence for no effect, and Fraser *et al.* [51] found that 37% of 494 ecologists reported collecting more data after checking whether results were statistically significant.

## Glossary

### Apparent context dependence:

relationships or outcomes appear to vary under different conditions, but variation is driven by issues related to confounding factors, statistical inference, and methodological differences that cause variation in the appearance of a relationship, not variation in the underlying causal relationship.

**Confounding factors:** confounding occurs when differences in Y associated with changes in X cannot be separated from other factors (C), that is, X and C are confounded such that C might simultaneously affect Y, obscuring the underlying X–Y relationship; also called ‘confounding variables’, ‘confounding features’ or ‘confounders’; a source of apparent context dependence.

**Context dependence:** variation in the sign or magnitude of an ecological relationship depending on the conditions under which the relationship occurs or is observed; also known as ‘contingency.’

**Design analysis:** a set of statistical calculations about possible study outcomes generated through hypothetical replications of a study that modify, for example, sample size, uncertainty, effect sizes, factors, and variables included in a study; can be used to calculate Type M and Type S error rates; can be prospective or retrospective; related to but broader than statistical power analysis.

**Gradient experiments:** multilevel experiments that lack replicates but instead span a wider gradient of environmental conditions (X axes) by maximising the diversity of conditions examined.

**Interaction effects:** interacting factors or variables (Z) modulate the X–Y relationship because the effect of X on outcome Y depends on the value of Z; also called ‘interaction modifications’ or ‘interactions’ in statistics; can be called ‘higher-order interactions’ in ecology; source of mechanistic context dependence where Z is the context in which the X–Y relationship varies.

**Invasive:** refers to alien (non-native, exotic) species introduced by humans outside of their natural biogeographic ranges with populations that spread over a wide range, reach high abundance, and often cause negative impacts.

**Mechanistic context dependence:** fundamental variation in a causal

Inaccurate estimates of X or Y can cause systematic bias in data, distorting estimated X–Y relationships. For example, observers with little experience may not detect or may misidentify species [22,53]. McClintock *et al.* [54] showed that even very low rates of false positive errors (1% of total records) can severely distort species occupancy predictions, over- or under-estimating distributions, and result in spurious X–Y relationships. Imprecise estimates cause random measurement error, increasing noise and uncertainty and decreasing statistical power. Unlike systematic bias, which has to be addressed during the observation process [55], effects of random measurement error can be mitigated by increasing sample size [22]. For example, in a search experiment for invasive orange hawkweed (*Hieracium aurantiacum*), Moore *et al.* [56] showed that detection probability for an average observer increased with increasing search effort.

**Type:** apparent; **source:** (iv) methodological differences

Apparent context dependence in the X–Y relationship can also arise if studies or models that are directly compared differ in methodological approach. This is distinct from the other sources of apparent context dependence because the X–Y relationship in the component studies could be estimated both accurately and precisely; rather, it is the way in which the studies have been compared that is inappropriate. Methodological differences, as defined in this paper, can arise because of differences in: study indicators, metrics, and scales; the values and heterogeneity of explanatory variables (i.e., the X-gradient examined); and research approaches and practices.

The X–Y relationship could vary if studies measure X or Y in different ways [57–59]. For example, invader occupancy and invader abundance can both indicate invasion level, but factors related to these two metrics can differ [60], meaning studies that use these different indicators of invasion level could reach different conclusions [61]. Composite indicators or classification-based indices may be particularly troublesome as the underlying metrics or criteria may be unclear and metrics may inadvertently be conflated [25,62]. For example, definitions of species invasiveness vary such that two studies, both examining traits related to species invasiveness, could inadvertently examine different dimensions of invasiveness (e.g., local abundance, spread rate, or habitat breadth) [25]. Studies could consequently reach different conclusions about traits linked to species invasiveness solely because of differences in the underlying Y variable (see Figure IC in Box 1) [61]. Similar problems could arise with indices representing – among many – diversity [63], resilience and stability [64], and ecosystem services [65], each of which can be calculated in numerous ways.

Even if the same metrics are used, studies may not be comparable if they were conducted at different levels or extents of X, or at different scales (both grain and extent, *sensu* [66]). For example, factors found to influence invasion at an early stage may not predict success at a later stage [67,68], as shown by Junaedi *et al.* [69], who found that invader seed mass, specific leaf area, and residence time were related to the naturalisation, but not spread, of alien plant species in tropical forests of Indonesia. Similarly, conclusions about the X–Y relationship can differ if the relationship is nonlinear and studies consider a different range of X values. For instance, a study that included only sites with low *Pinus nigra* biomass would find a positive relationship with grassland species richness in New Zealand, whereas a study with only high biomass sites would find a negative relationship (see Figure ID in Box 1) [70,71]. Because different processes can operate at different scales [72], relationships evident at fine scales can be lost at broad scales [73], relationships can shift from linear to non-linear [74], and slopes can change direction [3]. Such scale dependence can distort findings of meta-syntheses when component studies have been conducted at different scales, as is often the case [14].

Apparent context dependence can also stem from differences in research approaches and study systems (e.g., observer differences; whether a study is conducted in a laboratory or greenhouse,

relationship under different biotic, abiotic, and spatiotemporal conditions, which stems from interaction effects, such that the X–Y relationship depends on other (interacting) variable(s) (Z).

**Methodological differences:** refers to situations where studies observe and measure variables or relationships in different ways that are not directly comparable; a source of apparent context dependence.

**Statistical inference:** process of drawing conclusions about an underlying population based on a sample or subset of data from that population; in our typology, we use ‘statistical inference’ to also refer to the process of estimation (i.e., sampling of the data subset used in analysis); a source of apparent context dependence.

**Statistical power:** probability of finding an effect or relationship when one is present; a function of significance threshold, sample size, and effect size.

**Type I error:** rejection of a true null hypothesis (a false positive).

**Type II error:** failure to reject a false null hypothesis (a false negative).

**Type M error:** error in the magnitude of an estimated effect; also known as ‘exaggeration ratio.’

**Type S error:** error in the sign of an estimated effect.

**X:** independent (explanatory, predictor, causal) variable.

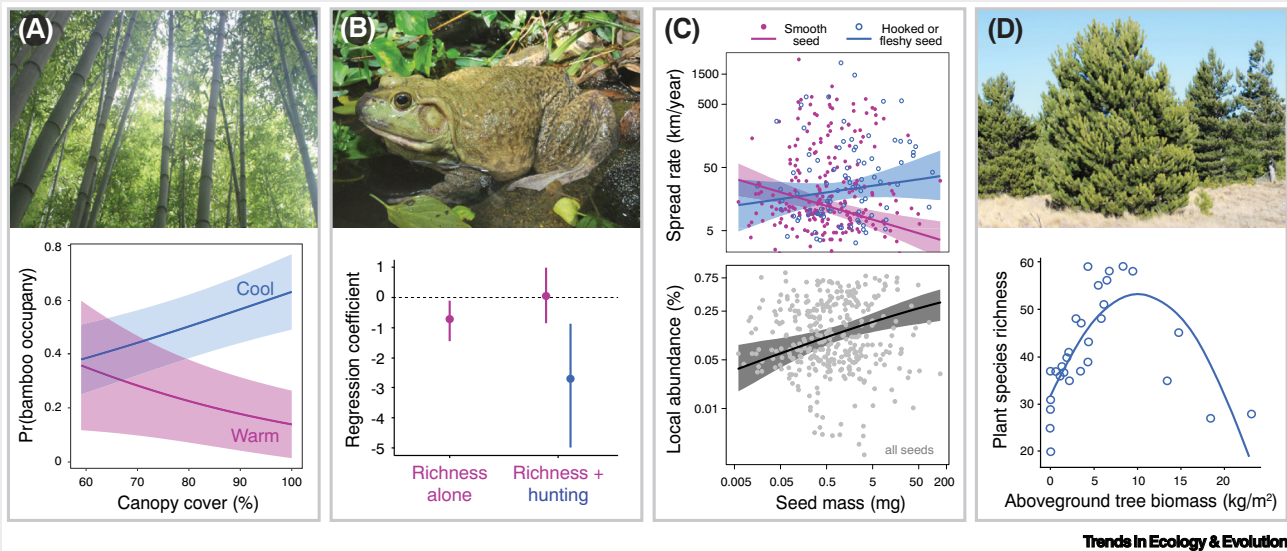
**X–Y relationship:** relationship between variable X and variable Y; X sometimes considered to causally affect Y.

**Y:** dependent (response, outcome) variable.



## Box 1. Context dependence in biological invasions

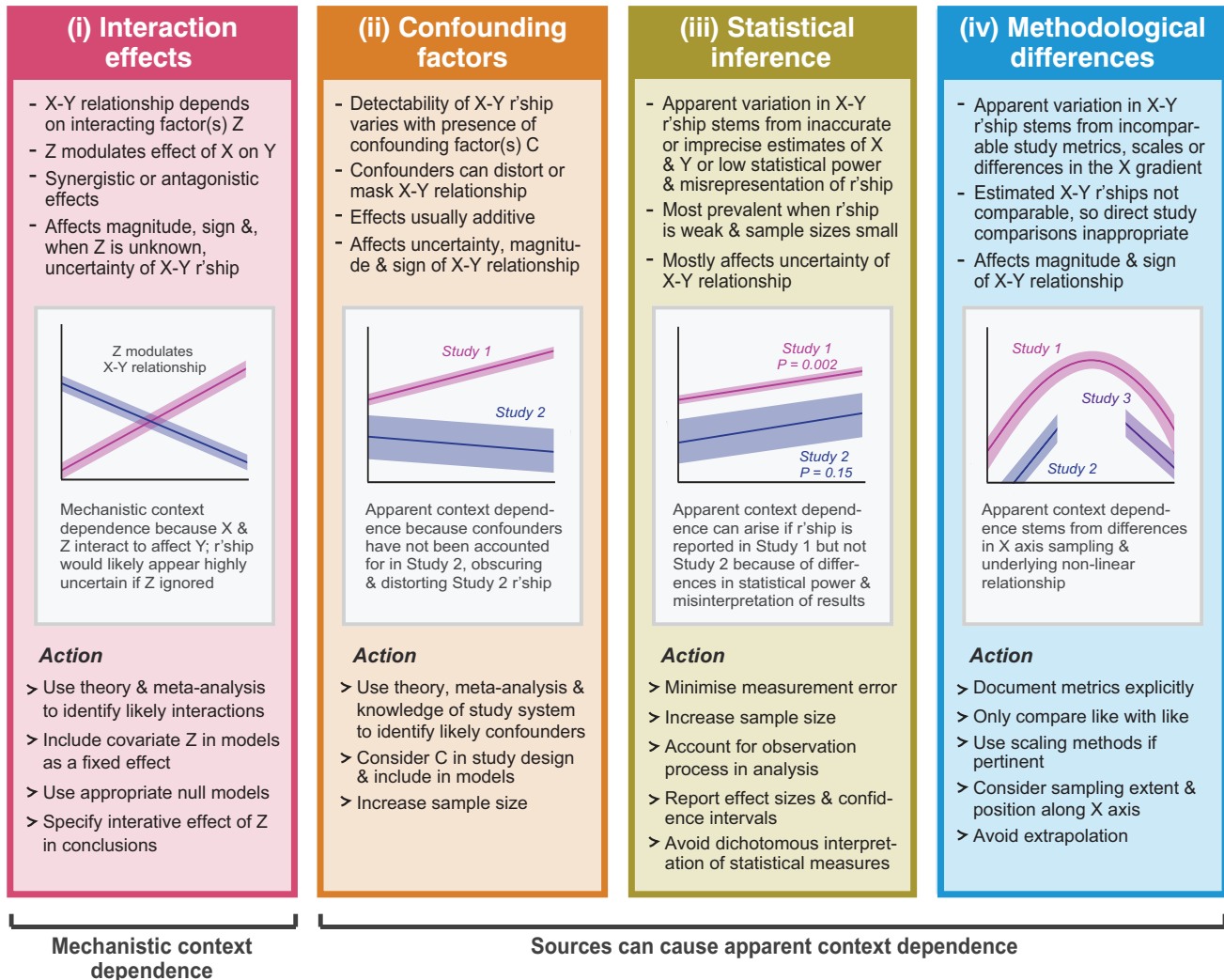
The context of biological invasions matters: it can determine whether, when, and where invaders fail or succeed; which systems are resistant or vulnerable to invasions; the impacts that invaders cause; and the approaches through which they can be managed. Despite robust understanding of the key drivers of invasion [103,104], empirical studies of plant invasion commonly find substantial variation in relationships where the magnitude, sign, and uncertainty of relationships varies both within and between studies (Appendix S1, Figures S1 and S2, and Tables S1 and S2). Context dependence may be especially prevalent in invasion ecology because of the diversity of contexts encountered, including ecoevolutionary characteristics of recipient ecosystems, introduction histories and the role of humans, invader traits, applied and fundamental research questions, and observational measures [60,67,117]. These contexts can modulate, or appear to modulate, the relationship between primary drivers of invasion (e.g., propagule pressure, time since invasion, disturbance) and outcomes of invasion (e.g., invader occupancy, abundance, impact and response to management; Figure 1). Because it is an applied discipline, there is a particularly pressing need to understand and overcome context dependence in invasion ecology: to predict future invasion and assess likely management efficacy, we need to be able to transfer results across studies, species, and regions; unless properly addressed, context dependence can inhibit such transferability.



**Figure 1.** Examples of different sources of context dependence in biological invasions. (A) Giant bamboo, *Phyllostachys bambusoides*, which is invasive in Japan, shows a positive relationship with canopy cover in cold regions but a negative relationship in warm regions, owing to interaction effects of light and temperature on bamboo occupancy (example of interaction effects) [26]. (B) Invasion success of bullfrogs, *Rana catesbeiana*, is negatively related to native frog species richness in eastern China, but this relationship disappears when the confounding effect of frog hunting is accounted for in a logistic regression model (confounding factors) [44]. (C) Across 236 alien herbs in southeastern Australia, the relationship between species seed mass and spread rate depends on whether seeds are smooth or hooked (upper panel) (interaction effects), but a different relationship is obtained if abundance, not spread rate, is used as a measure of species invasiveness (lower panel) (methodological differences) [61]. (D) Aboveground biomass of invasive *Pinus nigra* in New Zealand has a unimodal relationship with plant species richness (methodological differences) [70] (image redrawn from [71]). Photo credits: (A) Marco Schmidt, CC BY-SA 3.0, via Wikimedia Commons; (B) Ren-Jay Wang; and (D) Sarah Wyse.

using field experiments or observations) [10,53,75]. For example, the apparent paradox between native plant richness and alien plant richness – where a negative relationship tends to be observed in experiments and a positive relationship in observational studies [76] (but see [77]) – has been attributed (though not exclusively [78]) to lower environmental heterogeneity (and niche diversity) at small scales, which typify experiments, versus the higher heterogeneity at larger scales typical of observational studies [3]. While this explanation for observed variation in the relationship has wide support, a recent meta-analysis showed that ~70% of variation across 161 native–alien richness relationships could be attributed to article- and author-specific differences, suggesting the relationship observed depends strongly on author choices about study system and approach [4], including study grain size [78]. Many between-study differences can stem from issues related to interaction effects, confounding factors, and statistical inference (Figure 2) but – unless those sources of variation can be accounted for – they may be considered methodological differences.

## Four sources of context dependence



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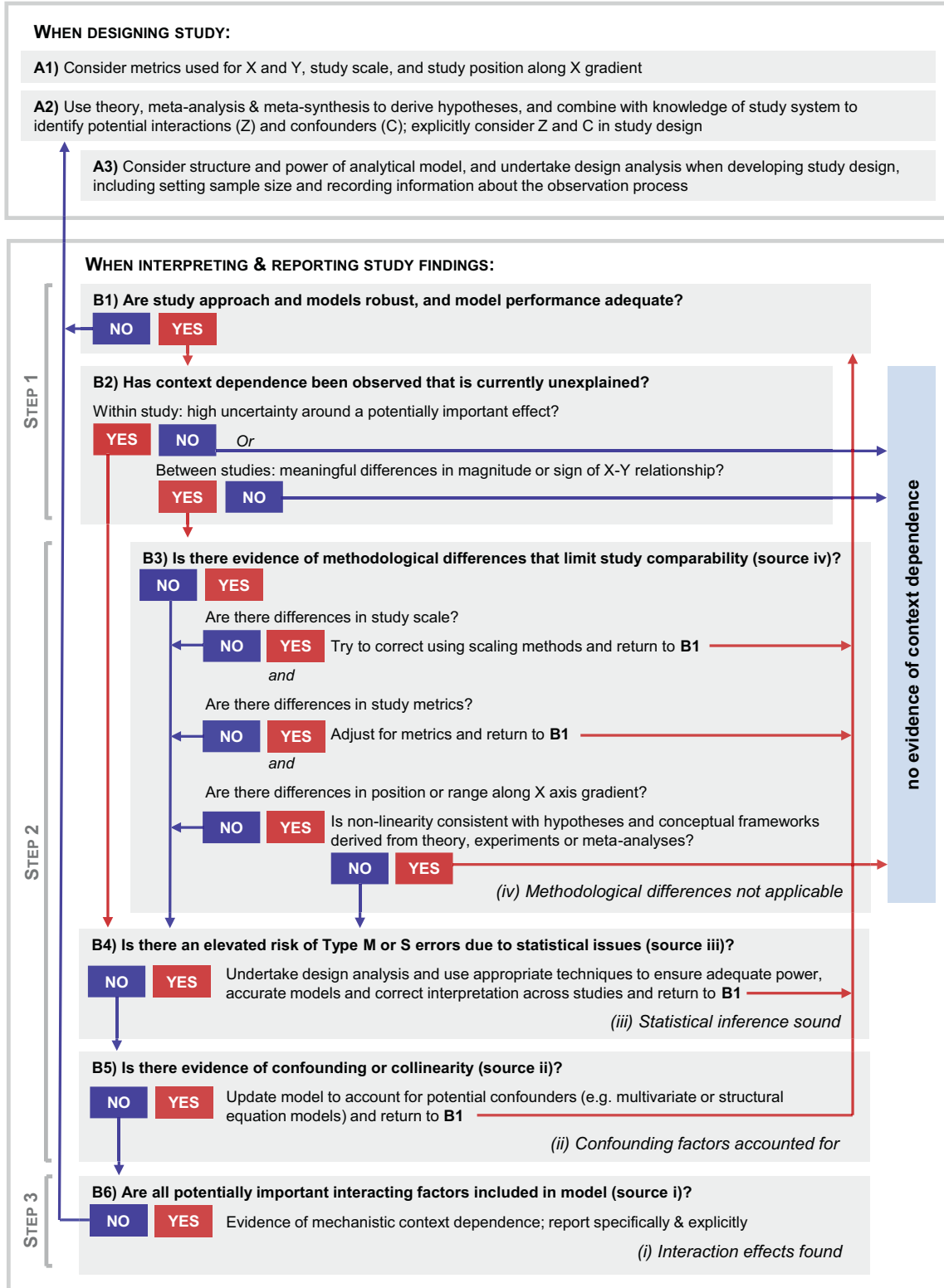
Figure 2. Four sources of variation in the relationship between independent variable X and dependent variable Y, with illustrative examples and actions that can reduce unexplained variation and the likelihood of apparent context dependence. Methodological differences (iv) are the easiest to address and confounding factors (ii) are arguably the hardest, because it is likely that multiple factors will affect ecological outcomes, not all of which can be accounted for. Once interacting factors are identified, variation from interaction effects (i) should be predictable. Variation can be the result of biological/ecological mechanisms (i) or study design and practice (ii–iv). The sources of variation are not mutually exclusive and are often interrelated and can manifest in various ways (Figure 1). White boxes show examples only; many other scenarios could occur, for example, different metrics for source (iv). "Relationship" sometimes abbreviated to "r'ship". See also Table S3.

### The way forward: getting on top of context dependence

It is inevitable that relationships will vary across space and time and across species, systems and studies. To identify interaction effects that underlie mechanistic context dependence, we need to distinguish fundamental (mechanistic) from apparent variation in the X–Y relationship (Figure 3).

#### Step 1: identify meaningful variation and ensure transparent research practice

If we could measure and model everything and do so accurately and precisely, we should notionally be able to predict every outcome based on its specific context. One of the challenges for



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(See figure legend at the bottom of the next page.)

### Box 2. Mechanistic context dependence and ecological theory

Even if apparent context dependence is discounted (see [Figure 3](#) in main text), understanding and predicting mechanistic context dependence is challenging. We posit that increased incorporation of interaction effects into ecological theory should increase understanding of mechanistic context dependence by providing (i) predictions and testable hypotheses that shape study designs, and (ii) a clear structure to contextualise and communicate research findings. The stress gradient hypothesis, which proposes that facilitation is more common in stressful environments and competition in less stressful environments [38], provides a good example [118]. Instead of having to describe that plant–plant relationships are context dependent, the stress gradient hypothesis provides a way to succinctly summarise these relationships in an accurate and informative way (e.g., [Figure 1A](#) in [Box 1](#)) and highlights the drivers of the observed context dependence.

Interaction effects are central to many leading hypotheses in ecology, including – but certainly not limited to – the stress gradient hypothesis [38], stochastic niche theory [119], environmental stress model [120], and resource–enemy release hypothesis [121]. However, in invasion ecology at least, most hypotheses focus on single processes or concepts [103,104,115]. Combined with the widespread observation of context dependence, this suggests that there is somewhat of a mismatch between the complexity observed in nature and the complexity of ecological theory, and that greater incorporation of interaction effects into invasion theory would be helpful. For example, integration of ideas related to plant resource economics [36] and resource availability hypotheses [103] may help to explain context dependent trait-based relationships often observed along gradients of resource availability in plant invasion studies [24] (though trait–environment and trait–trait relationships are themselves highly variable and warrant more attention [122–124]). Along with invasion and functional ecology, other areas of ecology that may particularly benefit from greater theoretical consideration of interaction effects include predator–prey dynamics, forest management and restoration, biodiversity conservation, plant–soil feedbacks, and ecosystem services – areas where context dependence is frequently discussed ([Figure S2](#) and [Table S2](#) in the supplemental information online).

Myriad processes, concepts, and ‘discrete’ hypotheses could conceivably be candidates for integration [115], and the subsequent complexity could impede, rather than facilitate, greater generality [81,125]. One solution proposed for addressing complexity in community ecology is use of four ‘higher-level’ processes to unify multiple (‘lower-level’) mechanisms and hypotheses [114]. Clustering of 39 invasion hypotheses has similarly enabled five higher-level themes to emerge [103]. Distilling key processes through hierarchical approaches should help balance the tension between requisite and overwhelming complexity.

ecologists, and scientists more generally, is determining when variation needs to be understood or when it can effectively be disregarded and treated as noise (see [Outstanding questions](#)). Measures of model performance that compare explained with unexplained variance (e.g.,  $R^2$ ), or wide confidence intervals relative to effect sizes, can indicate when important covariates might have been overlooked and when unexplained interaction effects might exist ([Figure 3](#)) [73,79,80].  $R^2$  values reported in ecology papers are generally low (mean of 0.55 across 18 076 papers published between 1930 and 2010, declining over time [81]), which suggests that performance of many models could improve if additional relationships were considered.

Ecological importance should not be conflated with statistical significance [50,79]. While some people have argued for more stringent thresholds of statistical significance to reduce **Type I error** rates [82] (albeit with consequences for **Type II error** rates [83]), the merits of specifying uniform thresholds are questioned [84]. It is increasingly recognised that categorising findings as significant or non-significant can lead to unsupported claims of ‘no difference’ or ‘no association,’ so there is a strong movement to abandon notions and use of statistical significance altogether, regardless of whether frequentist, Bayesian, or other approaches are used [48]. Meta-analytic thinking and focusing on effect sizes and uncertainty (e.g., 95% confidence intervals) can help guard against Type M and S errors [46,85], reducing the prevalence of apparent context dependence that results from statistical inference ([Figure 2](#)) [46,49,50,85]. Prospective and retrospective **design analysis** can also increase the reliability of statistical inference by identifying studies at risk of high Type M or S errors and highlighting where sample sizes need to be greater [46,85]. Increasing sample sizes would also increase ability to detect confounding factors and interaction effects, especially if the additional samples were positioned strategically to, for example, maximise variability or extend the range of key variables [86].

### Step 2: distinguish mechanistic from apparent context dependence

Minimising or controlling for apparent context dependence during study design, analysis, and interpretation will enable greater focus on mechanistic context dependence ([Figure 3](#)). Careful

**Figure 3. Recommended actions to identify mechanistic context dependence that results from interaction effects.** Step 2 aims to minimise the three sources of apparent context dependence. Multiple sources of context dependence can apply. If a source cannot be discounted that does not provide evidence that there is apparent context dependence (sources ii–iv) or that there is no mechanistic context dependence (source i). Study refers to individual study or model. See the main text for supporting references.



articulation of metrics can help avoid apparent context dependence that arises from methodological differences, and scaling methods, such as rarefaction, can help ensure that findings are comparable where study scales differ [14,87,88]. Temporal scales and sequences are also important to consider [32].

Use of design analysis and avoiding dichotomous interpretations of statistical significance can help to overcome apparent context dependence stemming from statistical inference [46,48,49]. We can also try to predict the conditions under which measurement error will be elevated and adjust our study designs and approaches accordingly [89,90]. For example, information about survey conditions, ecosystem characteristics, observer experience, and species traits – all of which can affect model precision and accuracy [91,92] – can be included in our models [89,90].

Confounding can most effectively be dealt with during study design, though selection of statistical approaches less sensitive to effects of confounders can help [43,93,94]. Randomisation and stratification approaches, for example, aim to avoid collinearity by distributing confounders among experimental treatments or observational strata, effectively deconfounding X and C. Confounders can be identified using theory, results of previous studies, or expert knowledge [95]. Different methods are available for identifying different types of confounders [42,96,97]. For example, the change-in-estimate criterion, which defines confounders as variables that alter the unadjusted X–Y effect by a certain percentage (e.g. 10%), has proved useful for identifying influential confounders [98]. Correlation coefficients of  $|r| > 0.7$  indicate situations in which collinearity severely distorts model estimation [94]. As a measure of multicollinearity, variance inflation factor (VIF) values  $\geq 2.5$  are generally considered indicative of a high likelihood of confounding [42]. If potential confounders can be identified and measured, multivariate statistics can be used to statistically control for their effects on the X–Y relationship, study design permitting (e.g., see Figure 1B in Box 1). Methods of causal inference, such as structural equation modelling, provide a way to test postulated relationships between causal and confounding variables and to disentangle their effects [96].

Greater awareness and pursuit of transparent research practices, and greater support for studies that replicate other research, should also help minimise apparent context dependence. Although replication studies can help to distinguish false positives from true positives [47], and although 97% of surveyed ecologists view replication studies as important [99], replication studies currently only make up 0.023% of the ecological literature [100]. There are clear, workable recommendations for increasing transparency in ecology that can be adopted by funders, publishers, institutions, and individual scientists (e.g., preregistration of studies and data analysis plans, replication studies [47,49,79,101]), which should help generalities to emerge.

### Step 3: increase understanding of mechanistic context dependence

Many factors may interact to cause mechanistic context dependence [18,32,67], and understanding these interaction effects should be a research priority [10]. Hypotheses, theory, meta-analyses, and experiments should be used to guide which interaction effects are considered in study designs and analytical models, and to assess the likely validity of trends found (Figure 3) [19,45]. Even when the factors thought to affect a process have been thoroughly discussed – as is the case for biological invasions (Box 1) [5,67,102–105] – challenges remain for examining and synthesising across complex systems and moving from pattern detection to prediction (Box 2).

Among other approaches for studying mechanistic context dependence [7,106] (and higher-order interactions [107,108]), greater development and use of appropriate mechanistic null models provides a promising way forward [109]. **Gradient experiments** have also been touted as offering a paradigm shift for mechanistic modelling and predictive understanding of complex

systems [86]. Evidence suggests that moving from traditional replicated experiments to gradient experiments will increase our ability to detect, predict, and extrapolate interaction effects, especially when X variables are continuous, responses are non-linear, and sampling effort is limited [86] (but see [110]). Coordinated distributed experiments (e.g., NutNet [111]) and surveys (e.g., PlantPopNet [112]) are powerful approaches that help avoid the typical trade-off between case study precision, realism, and generality [113].

The potential complexity of mechanistic context dependence requires approaches for synthesising research findings. Hierarchical frameworks can be used to group and structure interaction effects, enabling trends to emerge even if disparate research approaches are used [103,104,114,115]. Effects of multiple environmental covariates can be condensed and rescaled in ‘biological terms’ by using biological proxies related to key ecological processes, such as using plant abundance to understand context dependent impacts of climate change on plant–plant interactions [15]. Studies that examine effects of the number of interacting factors, rather than effects of factor identity, can reveal general (‘meta’) ecological responses to multiple co-occurring factors [35,116].

When mechanistic context dependence is found, it is important to verify the causal basis of the interaction [31] and to specify the type of context and form of dependence. We therefore urge authors, where possible, to move beyond vague statements such as, ‘It is context dependent,’ and instead be explicit; for example, ‘The relationship depends on resource availability, moving from positive to negative with reduction in resource availability.’ Tying such statements with ecological theory can provide structure and signal generalities among studies (Box 2).

### Concluding remarks

Estimated relationships between variables can vary within and between studies due to ecological mechanisms and effects of study approaches, designs, and methodologies. Sources of apparent context dependence (confounding factors, statistical inference, and methodological differences) need to be considered (and ideally minimised) for causal X–Y relationships to be revealed. Mechanistic context dependence resulting from interaction effects is an important source of variability, essential for understanding and prediction in ecology. To increase understanding of mechanistic context dependence, we recommend (i) considering study design and model performance to assess whether key variables may have been missed, even if statistically ‘significant’ relationships are found; (ii) collectively using theory, experiments, observations, and statistics to assess whether observed context dependence is likely to be mechanistic or apparent; (iii) using gradient experiments and fit-for-purpose mechanistic null models to rigorously examine interaction effects; (iv) reducing the probability and impact of Type M and S errors by prioritising in-depth, smaller-scale studies over shallower, broader ones, and focusing on relationship effect sizes and uncertainty rather than statistical significance, ensuring that ecological importance is always the focus; and (v) explicitly considering multiple processes in the development of ecological theory (Box 2) [103,114,115]. Context dependence is an emerging issue and critical challenge in ecology that requires immediate attention (see Outstanding questions). By recognising the different ways in which context dependence can arise, we can better account for context dependence and reduce the prevalence of unexplained variation in ecology.

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No interests are declared.

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### References

- Li, S.-P. *et al.* (2015) The effects of phylogenetic relatedness on invasion success and impact: deconstructing Darwin's naturalisation conundrum. *Ecol. Lett.* 18, 1285–1292
- Pinto-Ledezma, J.N. *et al.* (2020) Testing Darwin's naturalization conundrum based on taxonomic, phylogenetic, and functional dimensions of vascular plants. *Ecol. Monogr.* 90, e01420
- Fridley, J.D. *et al.* (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88, 3–17
- Tomasetto, F. *et al.* (2019) Resolving the invasion paradox: pervasive scale and study dependence in the native-alien species richness relationship. *Ecol. Lett.* 22, 1038–1046
- Moles, A.T. *et al.* (2012) Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *J. Ecol.* 100, 116–127
- Anderegg, W.R.L. *et al.* (2020) Climate-driven risks to the climate mitigation potential of forests. *Science* 368, eaaz7005
- Song, C. *et al.* (2020) Towards a probabilistic understanding about the context-dependency of species interactions. *Trends Ecol. Evol.* 35, 384–396
- Miguel, M.F. *et al.* (2018) Context-dependency and anthropogenic effects on individual plant–frugivore networks. *Oikos* 127, 1045–1059
- Lynn, J.S. *et al.* (2019) Context-dependent biotic interactions control plant abundance across altitudinal environmental gradients. *Ecography* 42, 1600–1612
- Chamberlain, S.A. *et al.* (2014) How context dependent are species interactions? *Ecol. Lett.* 17, 881–890
- Kroeker, K.J. *et al.* (2017) Embracing interactions in ocean acidification research: confronting multiple stressor scenarios and context dependence. *Biol. Lett.* 13, 20160802
- Bracewell, S.A. *et al.* (2021) Latitudinal variation in the diversity–disturbance relationship demonstrates the context dependence of disturbance impacts. *Glob. Ecol. Biogeogr.* 30, 1389–1402
- Rohr, J.R. *et al.* (2020) Towards common ground in the biodiversity–disease debate. *Nat. Ecol. Evol.* 4, 24–33
- Spake, R. *et al.* (2021) Implications of scale dependence for cross-study syntheses of biodiversity differences. *Ecol. Lett.* 24, 374–390
- Vandvik, V. *et al.* (2020) Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proc. Natl. Acad. Sci. U. S. A.* 117, 22858
- Bradley, M. *et al.* (2020) Context dependence: a conceptual approach for understanding the habitat relationships of coastal marine fauna. *Bioscience* 70, 986–1004
- Fukami, T. (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annu. Rev. Ecol. Syst.* 46, 1–23
- Ewers, R.M. and Didham, R.K. (2006) Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev.* 81, 117–142
- Côté, I.M. *et al.* (2016) Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B* 283, 20152592
- Schoenle, L.A. *et al.* (2018) Understanding context dependence in glucocorticoid–fitness relationships: the role of the nature of the challenge, the intensity and frequency of stressors, and life history. *Integr. Comp. Biol.* 58, 777–789
- Sletvold, N. (2019) The context dependence of pollinator-mediated selection in natural populations. *Int. J. Plant Sci.* 180, 934–943
- Vetter, T.R. and Mascha, E.J. (2017) Bias, confounding, and interaction: lions and tigers, and bears, oh my! *Anesth. Analg.* 125, 1042–1048
- Shaweno, D. *et al.* (2018) Methods used in the spatial analysis of tuberculosis epidemiology: a systematic review. *BMC Med.* 16, 193
- Catford, J.A. *et al.* (2020) Community diversity outweighs effect of warming on plant colonization. *Glob. Chang. Biol.* 26, 3079–3090
- Catford, J.A. *et al.* (2016) Disentangling the four demographic dimensions of species invasiveness. *J. Ecol.* 104, 1745–1758
- Spake, R. *et al.* (2021) Applying the stress-gradient hypothesis to curb the spread of invasive bamboo. *J. Appl. Ecol.* 58, 1993–2003
- Albertson, L.K. *et al.* (2021) Uncovering patterns of freshwater positive interactions using meta-analysis: Identifying the roles of common participants, invasive species and environmental context. *Ecol. Lett.* 24, 594–607
- Briscoe Runquist, R.D. *et al.* (2020) Context dependence of local adaptation to abiotic and biotic environments: a quantitative and qualitative synthesis. *Am. Nat.* 195, 412–431
- Lawton, J.H. (1999) Are there general laws in ecology? *Oikos* 84, 177–192
- Simberloff, D. (2004) Community ecology: is it time to move on? *Am. Nat.* 163, 787–799
- Billick, I. and Case, T.J. (1994) Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* 75, 1529–1543
- Orr, J.A. *et al.* (2020) Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proc. R. Soc. B* 287, 20200421
- Cupples, J.B. *et al.* (2011) Dietary overlap and prey selectivity among sympatric carnivores: could dingoes suppress foxes through competition for prey? *J. Mammal.* 92, 590–600
- Feit, B. *et al.* (2019) Apex predators decouple population dynamics between mesopredators and their prey. *Ecosystems* 22, 1606–1617
- Rillig, M.C. *et al.* (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science* 366, 886
- Reich, P.B. (2014) The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75, 2–16
- Bertness, M.D. and Callaway, R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–193
- Soulé, M.E. *et al.* (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv. Biol.* 2, 75–92
- VanderWeele, T.J. and Shpitser, I. (2013) On the definition of a confounder. *Ann. Stat.* 41, 196–220
- Pearce, N. and Greenland, S. (2014) Confounding and interaction. In *Handbook of Epidemiology* (Ahrens, W. and Pigeot, I., eds), pp. 659–684, Springer New York
- Johnston, R. *et al.* (2018) Confounding and collinearity in regression analysis: a cautionary tale and an alternative procedure, illustrated by studies of British voting behaviour. *Qual. Quant.* 52, 1957–1976
- Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology* 84, 2809–2815

### Outstanding questions

How prevalent is apparent context dependence in ecology, and how often has it misled development of ecological theory or understanding?

For applied areas of ecology, including biological invasions, how often has failure to account for context dependence resulted in incorrect or suboptimal management or policy decisions?

What types of context dependence are most important, and which do we not consider enough?

How can we make robust generalisations when mechanistic context dependence is so common, with myriad factors potentially interacting?

Is there scope for a more standardised approach to examining context dependence in particular research fields, such as invasion ecology, perhaps by targeting key hypotheses?

How do we distinguish important from negligible context dependence? What is a meaningful level of variation in an ecological relationship? What is adequate and meaningful model performance in ecology?

How do we estimate realistic effect sizes, which underpin design analysis, when understanding is incomplete or rudimentary or where context dependence prevails?

How do we reconcile the trade-off between study breadth and depth, knowing that depth can increase understanding of mechanistic context dependence but at the cost of greater scope and generality? In-depth case studies that better account for context dependence will, in the long term, advance the research field by accumulating more reliable sources of information for meta-analyses and generalisations. Yet, high-impact journals and research funders often seem to favour broad-scale studies, which are more susceptible to apparent context dependence and less able to interrogate or reconcile mechanistic context dependence than in-depth, smaller-scale studies.

44. Yirming, L. *et al.* (2006) Why islands are easier to invade: human influences on bullfrog invasion in the Zhoushan archipelago and neighboring mainland China. *Oecologia* 148, 129–136
45. Mueller, K.E. *et al.* (2018) A tale of two studies: Detection and attribution of the impacts of invasive plants in observational surveys. *J. Appl. Ecol.* 55, 1780–1789
46. Gelman, A. and Carlin, J. (2014) Beyond power calculations: assessing type S (sign) and type M (magnitude) errors. *Perspect. Psychol. Sci.* 9, 641–651
47. Parker, T.H. *et al.* (2016) Transparency in ecology and evolution: real problems, real solutions. *Trends Ecol. Evol.* 31, 711–719
48. Amrhein, V. *et al.* (2019) Scientists rise up against statistical significance. *Nature* 567, 305–307
49. Lemoine, N.P. *et al.* (2016) Underappreciated problems of low replication in ecological field studies. *Ecology* 97, 2554–2561
50. Nakagawa, S. and Cuthill, I.C. (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol. Rev.* 82, 591–605
51. Fraser, H. *et al.* (2018) Questionable research practices in ecology and evolution. *PLoS One* 13, e0200303
52. Fidler, F. *et al.* (2006) Impact of criticism of null-hypothesis significance testing on statistical reporting practices in conservation biology. *Conserv. Biol.* 20, 1539–1544
53. Fitzpatrick, M.C. *et al.* (2009) Observer bias and the detection of low-density populations. *Ecol. Appl.* 19, 1673–1679
54. McClintock, B.T. *et al.* (2010) Unmodeled observation error induces bias when inferring patterns and dynamics of species occurrence via aural detections. *Ecology* 91, 2446–2454
55. Miller, D.A. *et al.* (2011) Improving occupancy estimation when two types of observational error occur: non-detection and species misidentification. *Ecology* 92, 1422–1428
56. Moore, J.L. *et al.* (2011) Estimating detection–effort curves for plants using search experiments. *Ecol. Appl.* 21, 601–607
57. Catford, J.A. *et al.* (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Glob. Chang. Biol.* 18, 44–62
58. Kikvidze, Z. *et al.* (2011) Importance versus intensity of ecological effects: why context matters. *Trends Ecol. Evol.* 26, 383–388
59. Parker, J.D. *et al.* (2013) Do invasive species perform better in their new ranges? *Ecology* 94, 985–994
60. Catford, J.A. *et al.* (2019) Traits linked with species invasiveness and community invasibility vary with time, stage and indicator of invasion in a long-term grassland experiment. *Ecol. Lett.* 22, 593–604
61. Palma, E. *et al.* (2021) Functional trait combinations reflect different demographic dimensions of invasiveness. *Ecology* 102, e03317
62. Fraser, H. *et al.* (2015) Consequences of inconsistently classifying woodland birds. *Front. Ecol. Evol.* 3, 83
63. Pavoine, S. (2020) *adiv*: an R package to analyse biodiversity in ecology. *Methods Ecol. Evol.* 11, 1106–1112
64. Van Meerbeek, K. *et al.* (2021) Unifying the concepts of stability and resilience in ecology. *J. Ecol.* 109, 3114–3132
65. Neugarten, R.A. *et al.* (2018) *Tools for Measuring, Modelling, and Valuing Ecosystem Services: Guidance for Key Biodiversity Areas, Natural World Heritage Sites, and Protected Areas*, IUCN World Commission on Protected Areas <https://doi.org/10.2305/IUCN.CH.2018.PAG.28.en>
66. Wiens, J.A. (1989) Spatial scaling in ecology. *Funct. Ecol.* 3, 385–397
67. Pyšek, P. *et al.* (2020) Macroecological Framework for Invasive Aliens (MAFIA): disentangling large-scale context dependence in biological invasions. *NeoBiota* 62, 407–461
68. Williamson, M. (2006) Explaining and predicting the success of invading species at different stages of invasion. *Biol. Invasions* 8, 1561–1568
69. Junaedi, D.I. *et al.* (2021) Traits explain invasion of alien plants into tropical rainforests. *Ecol. Evol.* 11, 3808–3819
70. Dickie, I.A. *et al.* (2011) Ecosystem service and biodiversity trade-offs in two woody successions. *J. Appl. Ecol.* 48, 926–934
71. Sapsford, S.J. *et al.* (2020) Towards a framework for understanding the context dependence of impacts of non-native tree species. *Funct. Ecol.* 34, 944–955
72. Chase, J.M. *et al.* (2020) Biodiversity conservation through the lens of metacommunity ecology. *Ann. N. Y. Acad. Sci.* 1469, 86–104
73. Berlow, E.L. (1999) Strong effects of weak interactions in ecological communities. *Nature* 398, 330–334
74. Chase, J.M. and Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416, 427–430
75. Verheyen, K. *et al.* (2018) Observer and relocation errors matter in resurveys of historical vegetation plots. *J. Veg. Sci.* 29, 812–823
76. Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176
77. Beaury, E.M. *et al.* (2020) Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecol. Lett.* 23, 476–482
78. Peng, S. *et al.* (2019) Correlation of native and exotic species richness: a global meta-analysis finds no invasion paradox across scales. *Ecology* 100, e02552
79. Fidler, F. *et al.* (2018) Improving the transparency of statistical reporting in *Conservation Letters*. *Conserv. Lett.* 11, e12453
80. Nakagawa, S. and Schielzeth, H. (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol. Evol.* 4, 133–142
81. Low-Décarie, E. *et al.* (2014) Rising complexity and falling explanatory power in ecology. *Front. Ecol. Environ.* 12, 412–418
82. Benjamin, D.J. *et al.* (2018) Redefine statistical significance. *Nat. Hum. Behav.* 2, 6–10
83. Saltz, D. (2010) Statistical inference and decision making in conservation biology. *Isr. J. Ecol. Evol.* 57, 309–317
84. Lakens, D. *et al.* (2018) Justify your alpha. *Nat. Hum. Behav.* 2, 168–171
85. Altoè, G. *et al.* (2020) Enhancing statistical inference in psychological research via prospective and retrospective design analysis. *Front. Psychol.* 10, 2893
86. Kreyling, J. *et al.* (2018) To replicate, or not to replicate – that is the question: how to tackle nonlinear responses in ecological experiments. *Ecol. Lett.* 21, 1629–1638
87. Chase, J.M. *et al.* (2018) Embracing scale-dependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecol. Lett.* 21, 1737–1751
88. Kunin, W.E. *et al.* (2018) Upscaling biodiversity: estimating the species–area relationship from small samples. *Ecol. Monogr.* 88, 170–187
89. Altwegg, R. and Nichols, J.D. (2019) Occupancy models for citizen-science data. *Methods Ecol. Evol.* 10, 8–21
90. Louvrier, J. *et al.* (2018) Accounting for misidentification and heterogeneity in occupancy studies using hidden Markov models. *Ecol. Model.* 387, 61–69
91. Junaedi, D.I. *et al.* (2018) Traits influence detection of exotic plant species in tropical forests. *PLoS One* 13, e0202254
92. McCarthy, M.A. *et al.* (2013) The influence of abundance on detectability. *Oikos* 122, 717–726
93. McNamee, R. (2003) Confounding and confounders. *Occup. Environ. Med.* 60, 227
94. Dormann, C.F. *et al.* (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46
95. Lee, P.H. (2014) Should we adjust for a confounder if empirical and theoretical criteria yield contradictory results? A simulation study. *Sci. Rep.* 4, 6085
96. Shipley, B. (2016) *Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference with R* (2nd edn), Cambridge University Press
97. VanderWeele, T.J. and Ding, P. (2017) Sensitivity analysis in observational research: introducing the E-value. *Ann. Intern. Med.* 167, 268–274
98. Lee, P.H. (2014) Is a cutoff of 10% appropriate for the change-in-estimate criterion of confounder identification? *J. Epidemiol.* 24, 161–167
99. Fraser, H. *et al.* (2020) The role of replication studies in ecology. *Ecol. Evol.* 10, 5197–5207
100. Kelly, C.D. (2019) Rate and success of study replication in ecology and evolution. *PeerJ* 7, e7654
101. Parker, T.H. *et al.* (2018) Empowering peer reviewers with a checklist to improve transparency. *Nat. Ecol. Evol.* 2, 929–935
102. Richardson, D.M. and Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Prog. Phys. Geogr.* 30, 409–431

103. Enders, M. *et al.* (2020) A conceptual map of invasion biology: Integrating hypotheses into a consensus network. *Glob. Ecol. Biogeogr.* 29, 978–991
104. Catford, J.A. *et al.* (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* 15, 22–40
105. Buckley, Y.M. and Catford, J. (2016) Does the biogeographic origin of species matter? Ecological effects of native and non-native species and the use of origin to guide management. *J. Ecol.* 104, 4–17
106. Boyd, P.W. *et al.* (2018) Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change – a review. *Glob. Chang. Biol.* 24, 2239–2261
107. Mayfield, M.M. and Stouffer, D.B. (2017) Higher-order interactions capture unexplained complexity in diverse communities. *Nat. Ecol. Evol.* 1, 0062
108. Mickalide, H. and Kuehn, S. (2019) Higher-order interaction between species inhibits bacterial invasion of a phototroph-predator microbial community. *Cell Syst.* 9, 521–533.e510
109. Schäfer, R.B. and Piggott, J.J. (2018) Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Glob. Chang. Biol.* 24, 1817–1826
110. Chalcraft, D.R. (2019) To replicate, or not to replicate – that should not be a question. *Ecol. Lett.* 22, 1174–1175
111. Borer, E.T. *et al.* (2014) Finding generality in ecology: a model for globally distributed experiments. *Methods Ecol. Evol.* 5, 65–73
112. Smith, A.L. *et al.* (2020) Global gene flow releases invasive plants from environmental constraints on genetic diversity. *Proc. Natl. Acad. Sci. U. S. A.* 117, 4218–4227
113. Matthewson, J. and Weisberg, M. (2009) The structure of tradeoffs in model building. *Synthese* 170, 169–190
114. Vellend, M. (2016) *The Theory of Ecological Communities*, Princeton University Press
115. Latombe, G. *et al.* (2021) Mechanistic reconciliation of community and invasion ecology. *Ecosphere* 12, e03359
116. Harpole, W.S. *et al.* (2016) Addition of multiple limiting resources reduces grassland diversity. *Nature* 537, 93–96
117. Novoa, A. *et al.* (2020) Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. *Biol. Invasions* 22, 1801–1820
118. Maron, J.L. *et al.* (2014) Disentangling the drivers of context-dependent plant–animal interactions. *J. Ecol.* 102, 1485–1496
119. Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. U. S. A.* 101, 10854–10861
120. Silliman, B.R. and He, Q. (2018) Physical stress, consumer control, and new theory in ecology. *Trends Ecol. Evol.* 33, 492–503
121. Blumenthal, D.M. (2006) Interactions between resource availability and enemy release in plant invasion. *Ecol. Lett.* 9, 887–895
122. Shipley, B. *et al.* (2016) Reinforcing loose foundation stones in trait-based plant ecology. *Oecologia* 180, 923–931
123. Verberk, W.C.E.P. *et al.* (2013) Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshw. Sci.* 32, 531–547
124. Mitchell, D.J. and Houslay, T.M. (2021) Context-dependent trait covariances: how plasticity shapes behavioral syndromes. *Behav. Ecol.* 32, 25–29
125. Smith, R.A. *et al.* (2002) The high cost of complexity in experimental design and data analysis: type I and type II error rates in multiway ANOVA. *Hum. Commun. Res.* 28, 515–530