13 Tens Rule

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Abstract

The tens rule became a popular invasion hypothesis in the 1990s and is still widely used today, even though empirical support has been mixed from the beginning and the number of studies questioning it has been increasing in the past decade. Also, the rule is not based on a model or other defensible concept or argument. Here we divide the tens rule into two more specific sub-hypotheses: the *invasion tens rule* and the *impact tens rule*, where the former predicts that about 10% of species successfully take consecutive steps of the invasion process, and the latter that about 10% of established non-native species and about 1% of all introduced non-native species cause significant detrimental impacts. A quantitative meta-analysis of 102 empirical tests of the tens rule from 65 publications shows no support for this hypothesis. Looking at the invasion tens rule and comparing different taxonomic groups, about 25% of non-native plants and invertebrates, and about 50% of non-native vertebrates are on average successful in taking consecutive steps of the invasion process. We thus suggest replacing the invasion tens rule by two taxon-dependent hypotheses: the *50% invasion rule* for vertebrates and the *25% invasion rule* for other organisms, particularly plants and invertebrates. The impact tens rule is not supported by currently available evidence, either, and more data are needed before a reasonable alternative hypothesis can be formulated. In a nutshell, we suggest abandoning the tens rule and using the 50% invasion rule for vertebrates and the 25% invasion rule for other organisms. These hypotheses provide new standards that are supported by currently available data and against which future data can be tested.

Introduction

The tens rule posits that about 10% of species successfully take consecutive steps of the invasion process: circa 10% of species transported beyond their native range will be released or escape in the wild (they are called introduced species or casuals); about 10% of these introduced species will be able to establish viable populations in the wild (they are often called naturalized species); and about 10% of species established will become invasive/pest species (Williamson and Brown, 1986; Williamson, 1993, 1996; Jeschke *et al*., 2012; Jeschke, 2014). This rule became popular in the late 20th century

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and has been very influential within the field of invasion biology and beyond. It can be found in many popularizations (e.g. Kegel, 2013) and exhibitions (e.g. in the botanic garden in Potsdam, Germany) and has also been applied to genetically modified organisms (Regal, 1993; Williamson, 1993). The probability of a species transiting through the invasion process is a highly important parameter for ecological–economic cost–benefit models on the usefulness of actions such as border controls, and these models are sensitive to the precision of this probability (Keller *et al.*, 2007). It is thus not surprising that the tens rule has received considerable attention.

Yet this rule has several limitations and shortcomings. In particular, the proposed 10% value was not based on a model or other defensible concept or argument – it was simply picked on the basis of the idea that most non-native species will not be able to pass through the invasion process and have no significant impact. However, this idea was not further conceptualized or formally developed.

Another difficulty with this rule is that the invasion process to which it is linked has been differently defined by different authors. A particular challenge is that 'impact' is not really part of the invasion process because non-native species can have impacts during any stage of their invasion. Although their impact tends to increase through the invasion process, non-native species can have impacts directly after their arrival in the exotic range – think about a parasite or pathogen as an example (Ricciardi and Cohen, 2007; Ricciardi *et al.*, 2013; Jeschke *et al.*, 2013, 2014; Chapter 1, this volume). We thus follow Blackburn *et al.* (2011) and Jeschke *et al.* (2013) in not integrating 'impact' into the invasion process, but considering the following stages of this process: (i) *transport* to exotic range → (ii) *introduction* (release or escape into the environment) → (iii) *establishment* of a least one self-sustaining population → (iv) *spread*. These stages are as in Blackburn *et al.* (2011).

Because 'impact' is not a stage of the invasion process, we discriminate two different variants, i.e. sub-hypotheses, of the tens rule. The *invasion tens rule* (first sub-hypothesis) is restricted to the three outlined transitions between invasion stages. In addition, the suggestion that about 10% of established non-native species cause a significant detrimental impact (either on ecology/biodiversity, socioeconomics or human health) and that about 1% of all introduced species cause a significant detrimental impact can be termed the *impact tens rule* (second sub-hypothesis). We decided to devote attention to the impact tens rule in this chapter because it has been relatively unexplored thus far compared to the invasion tens rule (the latter can also be termed tens rule *sensu stricto*). Furthermore, Strayer (2012) suggested, on the basis of empirical evidence, that about 3–30% of established invaders substantially affect ecosystem functioning, which is in line with the impact tens rule. Please note that the suggestion that 1% of all introduced species cause a significant detrimental impact has not been made explicit in the context of the tens rule before.

A further difficulty with the tens rule is that its predictions are sensitive to the spatiotemporal scale of interest. Regarding the temporal scale, if more time passes, then typically more introduction events of a given species will have occurred for a given region, either intentionally or unintentionally, and some of these introductions will have been successful. One of the predictions of the tens rule is, as outlined above, that about 10% of all introduced species will establish themselves. When researchers tested this prediction for a given region and a given set of species, let's say in the 1990s, and another team of researchers repeats the study with the same set of species today, they will find a higher establishment success (defined as the number of established species divided by the number of introduced species) today than in the earlier study, assuming that no or few of the originally established species later died out. The tens rule predicts that establishment success is about 10% and does not qualify the temporal scale, yet the establishment success of a species is actually time dependent (see also Richardson and Pyšek, 2006).

Establishment success is also dependent on the spatial scale. For instance, let's again look at two teams of researchers that investigate establishment success. Team A has chosen the small European country Liechtenstein as their focal region, whereas team B has chosen the USA. If a given species has been introduced to both countries multiple times, there is a higher chance that it was able to find a suitable environment in the USA where a larger suite of environmental conditions are available as well as more species as potential positive interaction partners of the non-native species (e.g. prey, food or mutualists). In other words, there is a higher probability that the ecological niche of the non-native species fits somewhere in the USA compared to Liechtenstein. It is even more extreme when comparing global establishment success (of species introduced anywhere) with small-scale establishment success. To our knowledge, this limitation of the tens rule in its applicability across spatial scales has been largely overlooked thus far.

Given all these limitations, it might not surprise that the tens rule has received mixed empirical support at best (Jeschke *et al.*, 2012; Jeschke, 2014 and references therein). Another complication when testing this hypothesis is that reliable data about establishment success are often hard to find because numbers of introduced species that did not establish are often unknown (failed introductions; Jeschke, 2009; Rodriguez-Cabal *et al.*, 2009). They are typically best known for mammals and birds, which is why most studies addressing the tens rule have been done for vertebrates, in contrast to most other invasion hypotheses where the majority of studies focus on plants (Jeschke *et al.*, 2012; Chapter 17, this volume).

Despite its limitations, the tens rule has remained a major hypothesis of the field and is still widely used today. For instance, in a recent survey among >350 experts by Enders *et al.* (2018), it was the seventh best-known out of 33 invasion hypotheses featured in the survey. In this chapter, we use a quantitative meta-analytic approach to address the following questions: (i) what is the level of support for the tens rule and its sub-hypotheses? (ii) Does the level of support differ among major taxonomic groups and habitats? (iii) Has the level of support changed over time?

Methods

Hierarchy of hypotheses

Using the hierarchy-of hypotheses (HoH) approach (Chapters 2 and 6, this volume), we divided the tens rule into the invasion tens rule and the impact tens rule as follows:

- Invasion tens rule: about 10% of species successfully take consecutive steps of the invasion process.
  i. Transport → introduction: about 10% of the transported non-native species are released or escape.
  ii. Introduction → establishment: about 10% of the introduced species are establishing themselves.
  iii. Establishment → spread: about 10% of the established species are substantially spreading from their point(s) of introduction.
- Impact tens rule:
  iv. About 10% of established non-native species cause a significant detrimental impact (i.e. they have harmful ecological, socio-economic or human health effects); this sub-hypothesis thus relates to the transition establishment → impact/pest species.
  v. About 1% of all introduced non-native species cause a significant detrimental impact; this sub-hypothesis thus relates to the transition introduction → impact/pest species.

Dataset

We updated a previously collected dataset (Jeschke *et al.*, 2012) for our analyses. This dataset originated from a systematic literature search done in 2010 using the string '(tens rule OR establishment success) AND (alien OR exotic OR introduced OR invasive

OR naturali?ed OR nonindigenous OR non-native)'; see Jeschke *et al.* (2012) for details. The dataset includes 75 empirical tests of the tens rule from 53 publications (publications testing two or three transitions in the invasion process were considered as two or three tests of the tens rule). Most of these tests relate to the sub-hypothesis on the transition introduction → establishment (which is generally well investigated and was also emphasized in the search string).

Because the impact tens rule is not well represented in this previous dataset, we updated the dataset with an additional literature search focused on this hypothesis. We searched the Web of Science on 8 December 2016 using the following string: 'tens rule AND (impact* OR effect* OR affect* OR chang* OR ecosystem service* OR harm* OR pest*) AND (alien OR exotic OR introduced OR invasive OR naturali?ed OR nonindigenous OR non-native)'. In addition, we searched for publications in the Web of Science that cited Vilà *et al.* (2010), which is a key paper on the proportions of non-native species with impacts. Finally, one paper in Jeschke *et al.*'s. (2012) dataset was replaced: the 2nd edition of the catalogue of alien plants of the Czech Republic (Pyšek *et al.*, 2012) replaced the 1st edition (Pyšek *et al.*, 2002). The combined and updated dataset includes a total of 102 empirical tests from 65 publications. It is freely available online at www.hi-knowledge.org.

Quantitative meta-analysis

We applied a quantitative approach to compare the predictions of the tens rule with the data reported in the 102 tests we identified. For each sub-hypothesis, we calculated weighted means and 95% confidence intervals (CIs) for the percentage of species making the transition. We thereby followed a random-effects meta-analytic approach, using the DerSimonian–Laird method as implemented in the OpenMetaAnalyst software (Wallace *et al.*, 2012), which in turn uses the metafor package in R (Viechtbauer, 2010). After having calculated the means and CIs in this way, we compared these to the 10% value predicted by the tens rule and the 5–20% range suggested by Williamson (1996); in the case of the transition introduction → impact/pest species, the comparison was done with the 1% prediction by the tens rule. We also compared the values across taxonomic groups, habitats and the time when empirical tests were published.

Results and Discussion

What is the level of support for the tens rule and its sub-hypotheses?

Neither the tens rule nor its sub-hypotheses are empirically supported by currently available evidence (Fig. 13.1). About two-thirds of the empirical tests in our dataset have focused on the invasion tens rule, the majority of these in turn on the transition introduction → establishment: about half of all empirical tests of the tens rule have focused on this sub-sub-hypothesis. The observed average percentage of species making this transition is >40% and thus more than four times larger than the tens rule's prediction; the difference is also statistically significant (Fig. 13.1). It is similar for the transition establishment → spread, where the observed percentage of species making the transition is >30% and thus more than three times larger than the prediction. The situation is less clear for the transition transport → introduction for which our dataset includes the lowest number of studies.

In the case of the impact tens rule, we observed that on average about 1 out of 4 established non-native species have a significant detrimental impact, which is again significantly more than the 1 out of 10 species predicted (Fig. 13.1). The discrepancy between observation and prediction is even larger for the transition introduction → impact/pest species: here, we observed that on average about 16 out of 100 alien species have a significant detrimental impact, whereas the impact tens rule predicts only 1 out of 100 alien species; hence there is a 16-fold difference here.

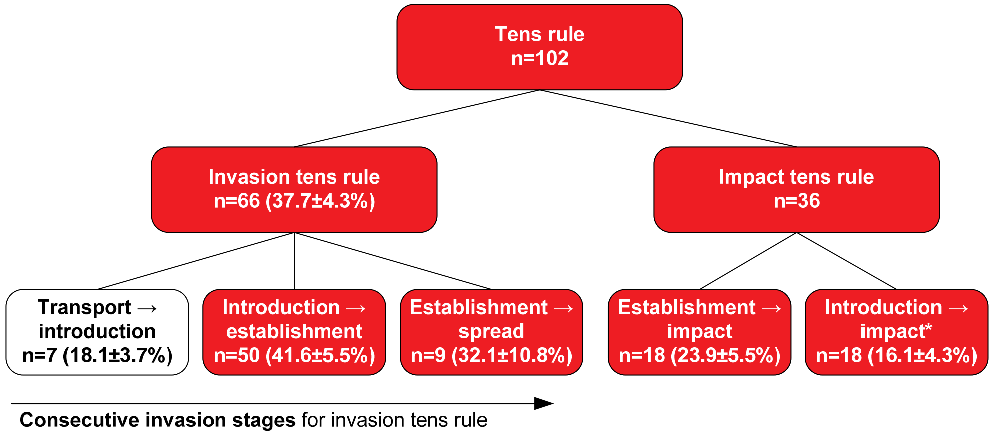

Fig. 13.1. The hierarchy of hypotheses for the tens rule. The boxes are colour coded: red indicates that the observed percentage of species making the transition is questioning the tens rule, i.e. the mean is >20%, the 95% confidence interval (CI) does not overlap with 10% and n ≥5; green (not existent) would indicate that the percentage of species making the transition is in line with the tens rule, i.e. the mean is between 5 and 20%, the 95% CI overlaps with 10% and n ≥5; and white is used for other cases, i.e. inconclusive data or n <5. Detailed information on the percentage of species making each transition and 95% CIs are provided in parentheses. *For the transition introduction → impact/pest species, the tens rule predicts that only 1% of the species make this transition; the colour coding has been applied accordingly. Because of this basic difference of the introduction → impact rule to the other rules, no quantitative summary values are provided for the impact tens rule and overall tens rule. They are coloured in red because their sub-hypotheses are contradicted by the available empirical data.

These findings are in line with previous results based on smaller datasets (Jeschke *et al.*, 2012; Jeschke, 2014 and references therein). Hence, currently available evidence does not support the tens rule. In the next section, we ask whether the tens rule is supported for some taxonomic groups or habitats, or whether this invasion hypothesis should be revised, replaced or completely abandoned.

Does the level of support differ among major taxonomic groups and habitats?

Even though the updated dataset has more data on the impact tens rule than the dataset of Jeschke *et al.* (2012), most data still focus on the invasion tens rule, and thus comparisons among taxonomic groups and habitats are particularly informative here. Our results show that much higher proportions of vertebrates than plants and invertebrates are successful in taking consecutive steps of the invasion process: on average, about every fourth plant (24%) and invertebrate (23%) is successful, whereas every second vertebrate (51%) succeeds (Fig. 13.2a). This difference is statistically significant, and the transition probabilities of all three taxonomic groups are significantly higher than the 10% predicted by the tens rule (Fig. 13.2a). These findings are largely in line with Jeschke *et al.* (2012) who also found significantly lower support for the invasion tens rule for vertebrates than for plants and invertebrates.

Regarding the impact tens rule, on average 18% of established plants have shown detrimental impacts, which is still significantly higher than 10% but much closer to the tens rule's prediction than the average values for invertebrates and vertebrates, which are both above 30% (Fig. 13.2b). Sample sizes are low, however, for the impact tens rule, hence more studies are needed to test whether these values hold true. This is

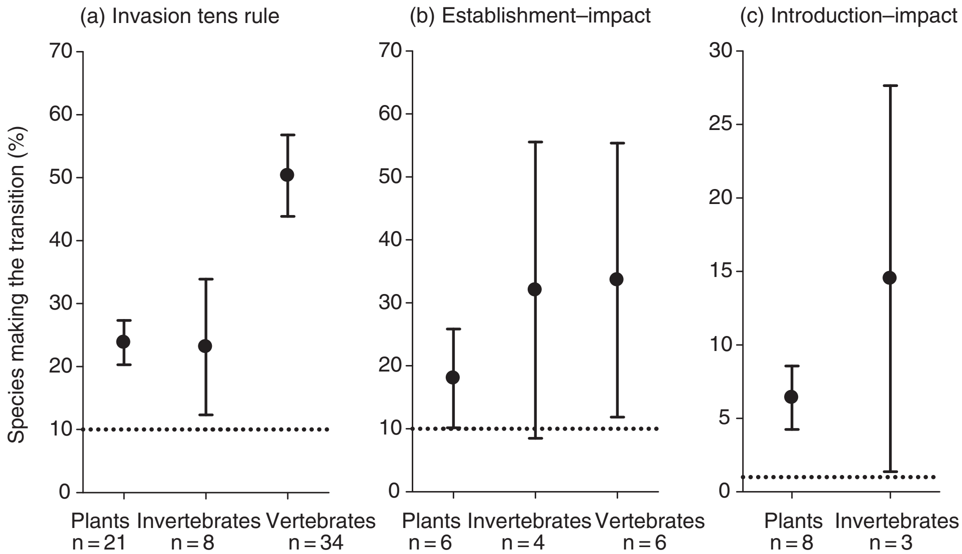

Fig. 13.2. Differences among major taxonomic groups in the percentage of species making the transitions (a) between consecutive stages of the invasion process (invasion tens rule, all three transitions combined), (b) establishment → impact/pest species and (c) introduction → impact/pest species (vertebrate studies are not shown here owing to the very low sample size of n = 2; panels b and c relate to the impact tens rule). Shown are means ± 95% confidence intervals. Sample sizes do not add up to 102 because empirical tests covering multiple taxonomic groups are not included. 'Plants' also include algae. Predicted percentages are indicated by dotted lines.

also true for the transition introduction → impact/pest species where data for vertebrates are very rare and thus not shown in Fig. 13.2c. Comparing plants and invertebrates, plants are again closer to the prediction of the tens rule than invertebrates. 'Closer' is relative, though, as on average 6% of the introduced plants have detrimental impacts, which is six times higher than the prediction; and 15% of the introduced invertebrates have detrimental impacts, which is 15 times higher than the prediction. These differences to the predicted value are also statistically significant (Fig. 13.2c).

The differences among major types of habitat (terrestrial, freshwater, marine) were slightly less pronounced (Fig. 13.3). Still, freshwater species were significantly more successful than terrestrial species in taking consecutive steps of the invasion process, with marine species being in between (invasion tens rule; Fig. 13.3a). This result is largely in line with Jeschke *et al.* (2012) who also found a significant difference between terrestrial and freshwater species. Regarding the impact tens rule, observed values were again consistently higher than predicted values, in most cases significantly so (Fig. 13.3b,c).

Has the level of support changed over time?

A decline in the level of support for six invasion hypotheses was reported by Jeschke *et al.* (2012), and decline effects have been previously reported from other disciplines, particularly medicine, psychology and evolutionary ecology (Lehrer, 2010; Schooler, 2011). Underlying reasons include publication biases, biases in study organisms or systems and the psychology of researchers (Jeschke *et al.*, 2012, and references therein).

Our quantitative analysis on a possible decline effect did not include the transition introduction → impact/pest species because

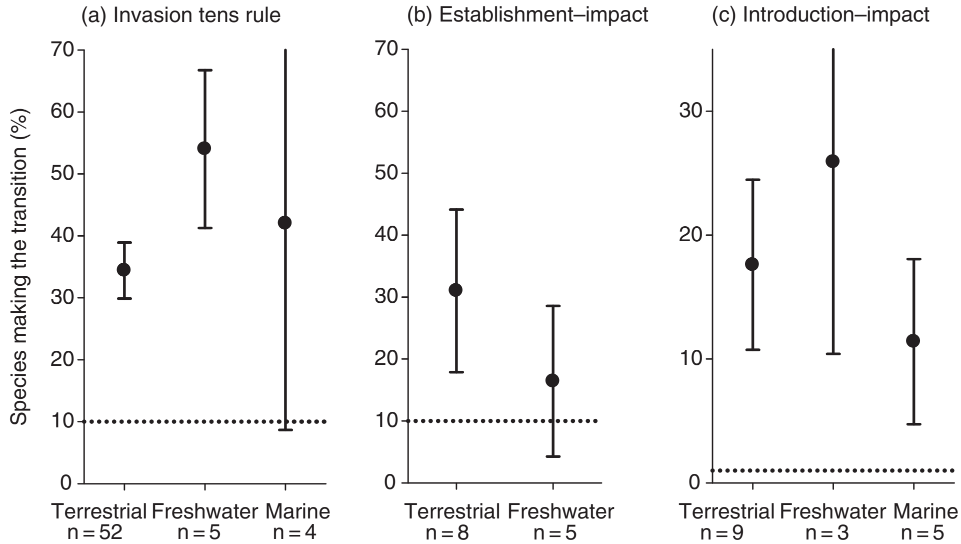

Fig. 13.3. Differences among major habitats in the percentage of species making the transitions (a) between consecutive stages of the invasion process (invasion tens rule, all three transitions combined), (b) establishment → impact/pest species (marine studies are not shown here due to the very low sample size of n = 2) and (c) introduction → impact/pest species (panels b and c relate to the impact tens rule). Shown are means ± 95% confidence intervals. Sample sizes do not add up to 102, as empirical tests covering multiple habitats are not included. Predicted percentages are indicated by dotted lines.

the prediction for this transition is 1%; thus data cannot be pooled with data for the other transitions where the prediction is 10%. The remaining data were used for this analysis. These 84 studies tended to show increasing transition success rates over time (Pearson's correlation coefficient $r = 0.37$, $p = 0.099$). Thus over time, observed transition success rates tended to increasingly differ from the 10% value predicted by the tens rule. One could interpret this tendency as a slight decline effect that was, however, not statistically significant.

Conclusions

In a nutshell, the tens rule lacks empirical support and neither of its sub-hypotheses depicted in Fig. 13.1 – the invasion tens rule and impact tens rule – are supported by currently available evidence. This is in line with previous studies based on smaller datasets (Jeschke *et al.*, 2012; Jeschke, 2014, and references therein). Nonetheless, the rule has remained a major hypothesis of the field and is still widely used today.

Jeremy Fox (2011), based on Quiggin (2010), used the term *zombie ideas* for hypotheses that are neither dead nor alive:

> Ideas, especially if they are widely believed, are intuitively appealing, and lack equally-intuitive replacements, tend to persist. And they persist not just in spite of a single inconvenient fact, but in spite of repeated theoretical refutations and whole piles of contrary facts. They are not truly alive—because they are not true—but neither are they dead. They are undead. They are zombie ideas.

It seems to us that the tens rule is a sort of zombie idea. On the basis of the findings reported here, we suggest that the invasion tens rule is replaced by two taxon-dependent hypotheses: the *50% invasion rule* for vertebrates and the *25% invasion rule* for other organisms, particularly plants and invertebrates. It should be kept in mind that these hypotheses share weaknesses with the tens rule, which are outlined in the Introduction above. One could argue that they should not be called 'rules' because of these weaknesses; however, we use this term, at least for now, in order to highlight that they are revisions of the tens *rule*. Like the tens rule but in contrast to other focal hypotheses in this book, they are data-driven and lack a formal theoretical foundation. But, in contrast to the tens rule, they are supported by currently available evidence.

Regarding the impact tens rule, more data are needed before it can be reasonably replaced by another hypothesis. The evidence that is currently available is too thin and the definitions of impact applied in available studies too variable (cf. Jeschke *et al.*, 2014) for an alternative hypothesis to be reasonably formulated at the moment. In any case, the percentage of introduced or established species with impact is not always the most important information because a single non-native species can have devastating impacts by itself. For example, an invasive lineage of the chytrid *Batrachochytrium dendrobatidis* is threatening a large number of amphibians worldwide, and rats, cats and other mammals are similarly threatening numerous vertebrate species (Bellard *et al.*, 2016). There is currently a lot of work focusing on invader impacts (reviewed in e.g. Jeschke *et al.*, 2014) and applications of the new IUCN Environmental Impact Classification for Alien Taxa (EICAT; Blackburn *et al.*, 2014; Hawkins *et al.*, 2015) might also prove useful for replacing the impact tens rule with a more adequate hypothesis.

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