



# A role for the sampling effect in invaded ecosystems

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Species loss and invasion of exotic species are two components of global biodiversity change that are expected to influence ecosystem functioning. Yet how they interact in natural settings remains unclear. Experiments have revealed two major mechanisms for the observed increase in primary productivity with plant species richness. Plant productivity may rise with species richness due to the increased amount of resources used by more diverse communities (niche complementarity) or through the increased probability of including a highly productive, dominant species in the community (sampling effect). Current evidence suggests that niche complementarity is the most relevant mechanism, whereas the sampling effect would only play a minor and transient role in natural systems. In turn, exotic species can invade by using untapped resources or because they possess a fitness advantage over resident species allowing them to dominate the community. We argue that the sampling effect can be a significant biodiversity mechanism in ecosystems invaded by dominant exotic species, and that the effect can be persistent even after decades of succession. We illustrate this idea by analyzing tree species richness–productivity relationships in a subtropical montane forest (NW Argentina) heavily invaded by *Ligustrum lucidum*, an evergreen tree from Asia. We found that the forest biomass increased along a natural gradient of tree species richness whether invaded by *L. lucidum* or not. Consistent with the sampling effect, *L. lucidum* invasion tripled total tree biomass irrespective of species richness, and monocultures of *L. lucidum* were more productive than any of the most species-rich, uninvaded communities. Hence, the sampling effect may not be restricted to randomly assembled, synthetic communities. We emphasize that studying invaded ecosystems may provide novel insights on the mechanisms underlying the effect of biodiversity on ecosystem function.

Synthesis

Niche complementarity and the sampling effect are the major mechanism that explain the positive relationship between biodiversity and net primary production. While the role of the former is clear, the latter is considered as a transient effect restricted to synthetic communities created experimentally. We explore the role of a dominant invasive species, *Ligustrum lucidum*, in a tree-species richness gradient of a natural mountain forest. Results are consistent with the idea that the sampling effect can be a relevant mechanism in natural ecosystems invaded by dominant exotic plant species and can persist in time.

## The sampling effect of biodiversity on productivity

Motivated by the potential consequences of global biodiversity loss, a growing number of experiments have been conducted to address the effects of reducing species diversity on ecosystem processes (Hector et al. 1999, Tilman et al. 2001, Scherber et al. 2010, Cardinale et al. 2012). After more than two decades of research, biodiversity and ecosystem functioning (BEF) experiments have shown that plant species richness generally has a positive effect on primary productivity (Hooper et al. 2005, Cardinale et al. 2012). The main explanation put forward for this relationship is the differential use of resources by species coexisting in a community,

a mechanism known as niche complementarity (Hooper et al. 2005, Loreau 2010). An alternative mechanism, the so-called sampling effect (also known as selection effect; Huston 1997, Loreau 2010), was identified as a potentially significant driver of BEF relations during the early stages of experiments using synthetic communities (Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012), but was suggested to contribute little to the observed effects of diversity in naturally assembled ecosystems (Wardle 1999, Flombaum and Sala 2008). Yet, is the sampling effect actually absent from natural systems? And, if present, is it always a transient effect that fades away with successional time? Here we argue that the sampling effect can be a relevant and

persistent effect in ecosystems invaded by highly competitive exotic species.

The sampling effect results from the increasing probability that a species with a high impact on ecosystem functioning occurs at a local community as the number of species is increased (Huston 1997, Tilman 1997). Under the sampling effect, the presence of a single species (or functional group), instead of the total number of species per se, is responsible for the observed increase in ecosystem functioning with diversity. For example, along a gradient of plant species richness created in N-limited grasslands, the presence of N-fixing plants (legumes) in the mixture explained the largest portion of the variation in net primary production (Huston et al. 2000). The sampling effect was initially interpreted as an experimental artifact of random community assembly studies using a limited species pool (Huston 1997, Wardle 1999, but see Tilman 1997). With the inception of new theory (Loreau and Hector 2001), and more sophisticated experimental designs, sampling effects were later recognized as an integral part of the total effect of biodiversity on ecosystem function (Tilman et al. 2001, Loreau 2010). Even so, the sampling effect remains as a relatively minor mechanism in most BEF experiments (Cardinale et al. 2007, Fargione et al. 2007, Flombaum and Sala 2008, Reich et al. 2012). Here we suggest that systems invaded by highly competitive exotic species may provide a different perspective.

### The sampling effect in invaded ecosystems

A few recent BEF experiments explicitly incorporated exotic plant species to evaluate whether ensembles of species not sharing a common evolutionary history exhibit the same underlying mechanisms as those of co-evolved, native species (Wilsey et al. 2009, 2011, Wang et al. 2013, Cook-Patton and Agrawal 2014). Simply put, exotic species may follow two alternative pathways to successfully invade an ecosystem; they can exploit unused resources, occupying 'empty niches' in the recipient community, or they can have a fitness advantage (e.g. enemy release) over resident native species when their niches overlap and competition is intense (MacDougall et al. 2009). In the first case, the effect of the invader on ecosystem function should be proportional to the amount of resources associated to the empty niche (e.g. water consumed during a period of the growing season). Thus productivity would be expected to increase with the number of exotic plant species occupying those niches, since more resources available in the local habitat could be used. Indeed, a BEF experiment mixing exotic and native species reported that the most important mechanism driving the effect of diversity on productivity was niche complementarity (Cook-Patton and Agrawal 2014). Alternatively, exotic species with a fitness advantage over resident species may become dominant ('strong invaders' sensu Ortega and Pearson 2005), having a large impact on ecosystem functioning (Rudgers et al. 2004, MacDougall et al. 2009). Then, productivity would be expected to increase as exotic species dominate communities along existing diversity gradients. Interestingly, in experimental ensembles of exotic species, productivity was found to increase with species richness as a result of the sampling effect, whereas in native species

mixtures the richness effect on productivity was driven by niche complementarity (Wilsey et al. 2009).

In spite of these recent efforts, the role of exotic species in BEF research remains open to novel questions. Ecosystems invaded by dominant exotic species may provide an opportunity to examine whether the sampling effect can be a major driver of productivity–diversity relations, beyond experiments with synthetic communities. An idealized natural experiment would consist of a local gradient of species diversity where the probability of finding the dominant exotic species is the same as for any other species at each level of diversity. If the sampling effect occurs, then three conditions should be met. We expect the invasive exotic species to 1) dominate biomass production regardless of the richness and composition of local communities, 2) be the most productive species in monoculture, and 3) be the primary driver of the increase in average primary productivity with species richness. However, if niche complementarity is the main mechanism, we expect 1) biomass production of the invasive exotic species be limited by uniquely accessed resources, so the invader would be unable to dominate community biomass, 2) the increase in biomass production with species richness not be related to the presence of the exotic species, and 3) high-diversity species mixtures be more productive than the most productive species in monoculture. In the following, we illustrate how the sampling effect may operate in a natural system, by focusing on the widespread invasion of *Ligustrum lucidum* (glossy privet) in 'Las Yungas' subtropical rainforests in Argentina.

### Testing for sampling effect in a natural biodiversity experiment

We hypothesized that the sampling effect is a major mechanism increasing forest community aboveground biomass along natural gradients of tree species richness that may include or not *L. lucidum* in the plot species pool. We reasoned that *L. lucidum* exerts a significant influence on the structure and functioning of these secondary forests, where it often contributes a large proportion of the standing biomass, affects water dynamics, and suppresses many native species (Lichstein et al. 2004, Grau et al. 2008, Aragón et al. 2014). The presence of *L. lucidum* would influence ecosystem function mostly through its large contribution to the forest canopy (sampling effect), in lieu of using extra untapped resources (niche complementarity). To test this hypothesis, we used data from a network of permanent monitoring plots established in secondary montane forests of Tucumán in northwestern Argentina (26°70'S, 65°35'W). The dataset comprises the species richness and aboveground biomass for all trees present in 141 forest plots (400 m<sup>2</sup> each) with 15, 25 and 45 years of succession after agricultural clearance and abandonment. We analyzed these data as the outcome of a manipulative BEF experiment, as if tree species richness was controlled for by the experimental design. The experiment thus consisted of a richness gradient with one to eight tree species per plot, out of a local pool of 17 species. We randomly subsampled 79 plots of which 32% contained *L. lucidum*, which allowed us to recreated the increased chance of finding *L. lucidum* as the number of tree species

per plot increased (Supplementary material Appendix 1 Table A1).

Our analysis supported the hypothesis that the sampling effect is an important driver of tree productivity in these secondary forests. Tree species richness and aboveground biomass were positively and significantly related (Fig. 1: full line) across the entire set of forest plots, suggesting that the diversity-productivity relationship held true in this natural experiment. However, this relationship was strongly influenced by the presence of *L. lucidum*. Firstly, plots invaded by *L. lucidum* had greater standing biomass ( $340 \pm 55$  tons  $\text{ha}^{-1}$ ) than those not invaded by this species ( $100 \pm 30$  tons  $\text{ha}^{-1}$ ; Fig. 1: dotted versus dashed line). Secondly, we expected that *L. lucidum* monocultures had greater biomass than those of other tree species, but our dataset was limited to test this prediction, since only one of 16 other species was present as a monoculture. Nevertheless, the flat biomass response to increasing species richness observed in *L. lucidum* invaded plots (Fig. 1: dotted line) can be interpreted as an upper bound to overall tree biomass in the study system. In other words, on average, invaded plots exhibited similarly high tree community biomass, irrespective of species richness. Thus, despite data limitations, *L. lucidum* appears to be more productive in monoculture than other tree species in the system.

Lastly, the presence of *L. lucidum*, and not tree species richness, accounted for most variation in overall tree canopy biomass across study plots ( $p < 0.0001$ ; Supplementary material Appendix 1 Table A2: ANCOVA). *Ligustrum lucidum* invasion tended to increase the diversity-biomass slope from  $17 \pm 9.3$  tons  $\text{ha}^{-1}$  species $^{-1}$  in plots free of the exotic, to  $27 \pm 17$  tons  $\text{ha}^{-1}$  species $^{-1}$  in invaded plots (Fig. 1),

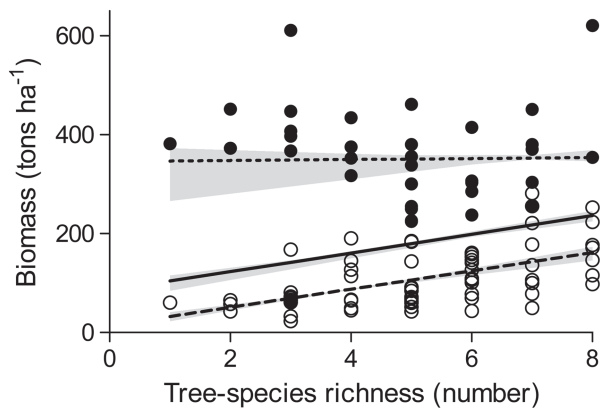


Figure 1. Total tree biomass as a function of tree species diversity in the subtropical montane forest of Tucuman, Argentina. Data analyzed as a BEF experiment showed that biomass increased with species richness for the entire set of forest plots, which may or may not be invaded by the exotic *L. lucidum* (full line; open and filled symbols;  $p < 0.04$ ). The positive tree biomass–richness relationship also held across forest plots not invaded by *L. lucidum* (dashed line; open symbols;  $p < 0.001$ ). Forest plots invaded by *L. lucidum* (dotted line; filled symbols) depicted the maximum biomass attained by the system, independent of species richness. Symbols represent all 141 plots from the available datasets. Lines and gray area represent the average and range of fitted regression from 79 subsampled plots. Ecosystems invaded with *L. lucidum*, filled symbols; not invaded, open symbols.

but the difference was not significant ( $p = 0.6$ ). More importantly, we found that the greatest biomass attained by any tree species mixture in uninvaded plots was much lower than that of *L. lucidum* monocultures (Fig. 1). This pattern is usually regarded as a critical test of the sampling effect in BEF experiments (Tilman et al. 2001, Cardinale et al. 2006). Therefore, our third prediction for the sampling effect was also supported.

We suggest that a sampling effect associated with the dominant presence of *L. lucidum* was the prevailing mechanism behind the observed increase in biomass with species richness in this subtropical forest. Our analysis also suggests that the sampling effect is not necessarily a transient mechanism, as observed in experiments with artificially assembled communities (Reich et al. 2012), but rather, that it can operate as a persistent biodiversity effect in natural ecosystems. Consistent with this interpretation, *L. lucidum* appears to have invaded secondary forests in the Tucuman mountains through a fitness advantage over native tree species, and not by occupying an empty niche. Most striking differences between *L. lucidum* and native species include its ability for early reproduction and for producing large amounts of fleshy-fruited, bird-dispersed seeds (Gurvich et al. 2005), which may provide a competitive advantage to the invader via resource pre-emption after disturbance. *Ligustrum lucidum* also share many vegetative traits with several resident tree species (Tecco et al. 2013), which suggests that it may occupy an ecological niche that is already well represented in the native community. Further, *L. lucidum* fitness advantage may stem from its faster growth rate and greater shade tolerance (Aragón and Morales 2003, Lichstein et al. 2004, Easdale et al. 2007). Nevertheless, niche differences and fitness advantages may interact with one another making it difficult to fully isolate their effects (e.g. root distribution and water use efficiency, Flombaum et al. 2014). Thus, even if niche complementarity plays a role in structuring these forest communities (Fig. 1: dashed line), the sampling effect would still be a major driver of the tree biomass–richness relationship.

## Conclusion

Niche complementarity, facilitation and sampling effect may all contribute to biodiversity effects on ecosystem functioning (Loreau and Hector 2001). Yet their relative roles may differ across systems in ways that remain to be uncovered (Paquette and Messier 2011). We have shown here that ecosystems invaded by a highly successful, exotic plant species may offer revealing examples of how and where the sampling effect may become an important mechanism in natural settings. Hence, contrary to prior views (Wardle 1999, 2016), the sampling effect need not be restricted to randomly assembled, synthetic communities. Ecosystems invaded by exotic species are ideal to examine the relevance of sampling effects because they provide links between deterministic (e.g. competition) and stochastic (e.g. colonization) processes influencing community assembly (Hooper et al. 2005). Moreover, non-invaded systems with a single native dominant species such as many northern temperate forests (Paquette and Messier 2011), tall-tussock grasslands (Perelman et al. 2003), *Nothofagus* forests in the Patagonian Andes (Piazza et al. 2016), and

*Spartina* saltmarshes around the globe (Doherty and Zedler 2014) could provide new evidence for the sampling effect as a relevant and persistent mechanism underlying biodiversity effects in nature. Indeed, we posit that the sampling effect may be inherent to the prominent functional role of foundation species (Ellison et al. 2005) in various ecosystems. Therefore, its contribution to ecosystem functioning might be more pervasive than previously thought, and deserves further empirical attention.

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Supplementary material (available online as Appendix oik-04221 at <[www.oikosjournal.org/appendix/oik-04221](http://www.oikosjournal.org/appendix/oik-04221)>). Appendix 1.