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SPECIAL FEATURE:
HARNESSING THE NEON DATA REVOLUTION

Six central questions about biological invasions to which NEON data science is poised to contribute

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Abstract. Biological invasions are a leading cause of rapid ecological change and often present a significant financial burden. As a vibrant discipline, invasion biology has made important strides in identifying, mapping, and beginning to manage invasions, but questions remain surrounding the mechanisms by which invasive species spread and the impacts they bring about. Frequent, multiscalar ecological monitoring such as that provided through the National Ecological Observatory Network (NEON) can be an important tool for addressing some of these questions. We articulate a set of major outstanding questions in invasion biology, consider how NEON data science is positioned to contribute to addressing these questions, and provide suggestions to help equip a growing contingent of NEON data users in solving invasion biology problems. We demonstrate these ideas through four case studies examining the mechanisms of plant invasions in the U.S. Intermountain West. In Case Study I, we evaluate the relationships between native species richness, non-native species richness, and probability of invasion across scales. In Case Studies II and III, we explore the relationship between environmental factors and non-native species presence to understand invasion mechanisms. Case Study IV outlines a method for improving the ability to distinguish invasive plants from native vegetation in remotely sensed data by leveraging temporal patterns of phenology. There are many novel elements in the NEON sampling design that make it uniquely poised to shed light on the mechanisms that can help us understand invasibility, prediction, and progression, as well as on the variability, longevity, and interactions of multiple invasive species' impacts. Thus, knowledge gained through analysis of NEON data is expected to inform sound decision-making in unique ways for managers of systems experiencing biological invasions.

Key words: biotic resistance; *Bromus tectorum*; *Eragrostis lehmanniana*; exotic plants; invasion biology; invasion impacts; invasive species; macroecology; macrosystems; National Ecological Observatory Network (NEON); scale; Special Feature: Harnessing the NEON Data Revolution.

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INTRODUCTION

Biological invasions are a leading cause of abrupt ecological change (Vitousek et al. 1997) and a strong source of economic burden to society (Pimentel et al. 2005, Crowl et al. 2008). The United States commits 2.5–3 billion dollars a year toward federal invasive species management efforts (National Invasive Species Council 2020). Furthermore, biological invasions are expected to continue increasing because they are exacerbated by other elements of global change, including climate change, land-use change, and increased globalization and trade (Dukes and Mooney 1999, Stachowicz et al. 2002, Levine and D'Antonio 2003, Bradley et al. 2010, Seebens et al. 2017, 2018, Auffret and Thomas 2019, Weiskopf et al. 2020). Despite the challenges presented by invasive species and their global importance in research and ecosystem management, improvements in our fundamental understanding of invasion biology are still needed to better ascertain their potential spread and impacts. It is particularly important to develop approaches that integrate information across temporal and spatial scales (Meyerson et al. 2019).

Many unanswered questions exist concerning biological invasions. Many of these questions can be categorized into two broad topics—Topic 1: the mechanisms of biological invasions (Buckley and Catford 2016) and Topic 2: the impacts of invasive species on recipient systems (Sutherland et al. 2013). Understanding the mechanisms enhances the ability to understand impacts, that is, the means by which invasive species introduce functional change to ecosystems (Parker et al. 1999, Strayer 2012). Understanding these key topics lays the groundwork for developing efficient treatment and prioritizing management efforts (Andersen et al. 2004). In order to gain that understanding, more and better data are needed—more frequent, more precise, and more comprehensive.

Data collected across spatial and temporal scales using consistent protocols are needed to fill critical knowledge gaps in invasive species research. The National Ecological Observatory Network (NEON) is a National Science Foundation (NSF)-sponsored continental-scale facility designed to collect and provide long-term, open-access ecological data to better understand how U.S. ecosystems are changing (Keller et al. 2008). For plant communities, NEON collects data on species cover, presence, and abundance through annual or biannual plot surveys at 47 terrestrial sites and from aquatic plant point count surveys in streams, lakes, and rivers that are collected multiple times per year at 34 sites. Field botanists make species-level identifications for plants that occur within a NEON sampling unit (e.g., plots, stream reaches), and determine whether the species origin is native or non-native. The observatory anticipates generating these data over a 30-yr timeframe. In some cases, NEON PhenoCam and airborne remote-sensing imagery may also document invasive plant presence, abundance, and other attributes.

NEON-enabled science is well-poised to inform important questions in invasion biology that have not previously been feasible to address. Early publications describing the intended applications of NEON highlight the ability to study invasive species in new ways as a key advantage of such a network (National Research Council 2004, Kampe et al. 2010, Kao et al. 2012). Yet only a small fraction of published literature utilizing NEON resources to date considers invasive species (Appendix S1: Table S1). This compels us to highlight some of the strengths of NEON-enabled science that are directly relevant to invasive species research.

Objectives

The purposes of this paper were to articulate a set of major outstanding questions in invasion ecology, to consider how NEON data science is positioned to help address these questions, and to help equip a growing contingent of ecologists and data scientists with the application of NEON data to solving invasion biology problems. Questions 1–3 are about invasion mechanisms (Topic 1), while questions 4–6 are primarily concerned with impacts (Topic 2). For each of these two topics, there is an overarching consideration of how answers to the questions can lead to management solutions. We offer four case studies as illustrative examples for how these topics might be studied using NEON data. We conclude with a discussion regarding applications for management as well as some advice for first-time NEON data users in invasion ecology. Indeed, many of the elements are in place to begin addressing parts of these and other questions central to the field, but a greater number of scientists with strong data skills is needed to maximize the opportunity at hand. We invite ecologists, managers, and data scientists of all career stages, everywhere, to embrace NEON data science in addressing these questions and others.

Invasion mechanisms

How does native diversity relate to invasibility?— Numerous hypotheses have been put forward regarding the potential invasibility of ecosystems, with one of the central factors being the role of the extant native biodiversity (Jeschke and Heger 2018). A central subject of debate has been the Biotic Resistance Hypothesis (Elton 1958), which posits that as the native biodiversity of a system increases, vulnerability to invasion decreases. Conceptually, the hypothesis suggests that if many niches in an ecosystem are already filled, then there are fewer opportunities for a new invader to establish. However, this hypothesis has been debated with evidence for both positive and negative correlations between native species richness and non-native species richness (Fridley et al. 2007). These discrepancies are driven by a variety of mechanisms such as biotic resistance, competitive exclusion (Kennedy et al. 2002, Davies et al. 2005), environmental filtering (Muthukrishnan et al. 2018), spatial heterogeneity (Davies et al. 2005), and statistical artifacts (Fridley et al. 2004). Different explanations for this inconsistency have also been presented focusing on spatial scale (Levine 2000, Stohlgren et al. 2003), methodological differences between observational and experimental approaches, and potential biases that arise from the types of systems in which research effort has been focused. The long-term data spanning systems, species, and scales, combined with detailed monitoring of abiotic conditions, produced by NEON could provide valuable information to address a number of persistent questions relating to diversity–invasibility relationships. Long-term monitoring is critical to disentangle if native diversity is a driver or a consequence of invasion and repeated sampling of specific locations can help discriminate between potential mechanisms (e.g., competitive exclusion vs biotic resistance; Muthukrishnan et al. 2018). Consistent sampling across a variety of ecosystem types can evaluate the generality or contingency of mechanisms across different habitats and would rarely be feasible for standard ecological research studies. Monitoring at multiple spatial scales with coordinated monitoring of abiotic conditions can facilitate comparison of potential drivers across scales. We investigate these ideas in Case Study I.

What environmental parameters are the best predictors of invasive species occurrence across locations/systems?— A central aim of ecology is understanding the spatial distributions of organisms. Researchers and managers alike seek to understand how environmental conditions affect the fitness of an organism and how those conditions can control their distribution (Elith and Leathwick 2009). Understanding these relationships is particularly valuable in the context of invasive species, as the ability to predict potential regions of spread is a critical issue. But for models and forecasts of distributions to be most effective, an understanding of all potentially constraining processes driving habitat suitability must be developed (Buckley et al. 2010). These relationships may vary between regions, so studies testing their effects across multiple sites are necessary to evaluate their robustness. Only then can confidence be placed in broader-scale models of distribution and spread. We investigate ancillary data representing environmental parameters as predictors of non-native species occurrence in NEON data through Case Studies II and III. Large environmental data sets and the potential for identification of a variety of different invasive species can allow for the evaluation of environmental features that align with increased invasion in general, as opposed to most studies which focus on factors relevant to a single or small number of invasive species of interest. More rigorously constructed understanding of habitat suitability can then be used to better inform spatial prioritization decisions for management actions and support regulatory decision-making and compliance (Sofaer et al. 2019).

*How can we better understand the rate of spread and transition through stages of invasion?—*The efficacy of management strategies to improve ecosystem resistance against invasion will depend in part on the progression through stages of invasion. Invasive plants (and other invasive organisms) generally advance through four stages of invasion: transport, colonization, establishment, and landscape spread (Richardson et al. 2000, Theoharides and Dukes 2007). Defining invasion stages in practical applications is complicated by the influence of environmental conditions, native diversity (Levine et al. 2004), Allee effects (Taylor and Hastings 2005), dispersal limitation (Martin and Canham 2010), and feedbacks (Reinhart and Callaway 2006) that inhibit or accelerate the invasion process. Additionally, the progression of invasion after landscape spread may follow boom-bust dynamics (Strayer et al. 2017, Závorka et al. 2018), therefore adding a fifth (possible) stage to the Theoharides and Dukes (2007) framework, "bust." It remains unresolved how common a "bust" stage is in the invasion process for plant communities. The ability to address multiple stages of invasion in a single study in order to evaluate how clear and consistent transitions are from one stage to the next and what implications or benefits there are to identifying those shifts remains a priority in the field (Theoharides and Dukes 2007). We investigate a method for enhancing the monitoring of the temporal dynamics and progression of an invasive species in Case Study IV.

*NEON-enabled science as a means to understand mechanisms of biological invasions.—*The multiscalar nature of NEON enables consistent monitoring of species occurrence and abundance in concert with a vast array of environmental conditions, from nutrient levels and soil moisture to human activity, disturbance events, weather, and climate. The integration of these data has the potential to build more precise and comprehensive expectations of environmental tolerance thresholds of invasive species.

NEON's nested plant diversity sampling design (Barnett et al. 2019) makes these data well-suited to explore questions of scale-dependent processes, including questions of invasibility. NEON terrestrial and aquatic sites span vast latitudinal, altitudinal, and other environmental gradients across the United States, allowing for the study of how heterogeneous conditions influence the correlation between native and non-native species occurrences to be explicitly examined. The terrestrial network offers a set of 47 opportunities for monitoring vegetation dynamics alongside numerous biophysical factors that may influence invasibility. NEON is thus well-suited to help reconcile different interpretations of mechanisms behind invasions, ultimately strengthening our ability to manage for resilient native diversity. Understanding the impacts of maintaining native diversity can help in both proactive conservation (Panetta and Gooden 2017) and best practices for recovery or restoration actions (Hulme 2006).

NEON is designed to monitor ecosystems frequently over multiple decades, which will be useful in resolving issues for specific management scenarios and contributing to the development of a general theory of invasion dynamics. The potential for observations that begin before the transport stage will allow for extremely valuable before-and-after studies to help define each subsequent stage of invasion. Identifying the onset of an invasion in a system and monitoring through early stages of spread are critical for risk assessment. That early monitoring can allow managers to anticipate what species may present serious risk to specific ecosystems (Meyers et al. 2020) and can help inform watch lists for jurisdictions within a given ecosystem (Reaser et al. 2020). Clear definitions of transitions from one invasion stage to the next will help prioritize and focus management actions to maximize efficient use of resources in controlling the spread of invasive species. The structure of NEON will facilitate opportunistic studies that can provide this early-stage monitoring and could clarify and refine existing definitions of where one stage of invasion ends and another begins. Different NEON sites fall into a range of invasion stages (e.g., Table 1). Some sites, such as the Jornada Experimental Range, have few introduced species, while others, such as Onaqui and Santa Rita Experimental Range, have fully passed the landscape spread stage for regionally dominant species (*Bromus tectorum* L. and *Eragrostis lehmanniana* Nees, respectively). Relatively intact sites will work well for monitoring the introduction

Table 1. Average abundance and richness of native and non-native species per plot at each of the NEON sites focused on in this study.

Site	Non-native cover (%)	Native cover (%)	Non-native species (n)	Native species (n)
Jornada	0.6	96.1	0.9	23
Moab	4	86.3	1.6	15.4
Onaqui	23.2	71.2	5.7	12.4
Santa Rita	9.6	80.9	3.6	45.6

Notes: Unidentified species are not included in the table, and thus, totals do not necessarily sum to 100%. For a table of all NEON sites, see Appendix S1: Table S2.

and spread of new species as they are first recorded in the data set. The sites that already have mature invasions are suited for detecting boom-bust dynamics.

Invasion impacts

How do impacts of biological invasions vary across environmental gradients?—Not all systems respond to invasions equally, but our understanding of why these differences exist remains limited. Clear definitions of ecosystem "impacts" must be given as a specified, measurable change in ecosystem structure and/or function in order to effectively inform management decisions (Strayer 2012, Vilà et al. 2019). The impacts of invasive species are context-dependent and may be subject to non-linear threshold effects (Sapsford et al. 2020). Thus, impacts must be monitored across environmental gradients and through time to quantify changes in the structure and function of ecosystems.

What are the long-term (multi-decadal) impacts of biological invasions?—An estimated two-thirds of biological invasion research has been conducted on time scales less than a single year, more than half of published studies do not report the initial date at which invasion in the study system began, and about half report on single rather than longitudinal measurements (Crystal-Ornelas and Lockwood 2020). Invasions may unfold slowly before sudden explosive population growth, and effects of invasion on the recipient system may be significantly lagged (Crooks 2005). Therefore, multi-year monitoring is needed to move toward drawing sound conclusions regarding impacts. There is also an opportunity to develop a broader understanding of the impacts of invasions by linking their effects to other processes that are being monitored and modeled over relatively long (multi-decadal) time scales. For example, vast areas of sagebrush in the Great Basin have become dominated by *B. tectorum* and, as a result, have reduced carbon storage in the region (Fusco et al. 2019, Nagy et al. 2020). Impacts of invasions will also be better understood through the adoption of a holistic, system-level approach. For example, considering shifts in community composition and measuring the resultant impacts on ecosystem functioning and services through numerous metrics allows for consideration of human values as well as objective ecosystem parameters (Muthukrishnan et al. 2020). A challenge that remains in implementing these considerations across broad scales is that without a true "control" to which invasion impacts can be compared, measured impacts cannot necessarily be attributed directly to the introduction of one species or group of species. Taken as a whole, these knowledge gaps necessitate a shift in research design, including funding mechanisms that can accommodate longer timeframes (Crystal-Ornelas and Lockwood 2020).

How do invaded ecosystems respond to multiple, potentially interacting invasions?—Another of the major limitations facing the field of invasion biology so far is that most of the research and management efforts are targeted to a particular invasive species (Strayer 2012, Crystal-Ornelas and Lockwood 2020), without a holistic understanding of multiple (potentially interacting) invasions and the full suite of impacts they have on the recipient system. It is also useful to consider how specific management actions might be more effective in specific ecosystems, including identification of ecosystem characteristics that are both more resistant to negative impacts and more resilient given the suite of feasible management actions available in that area. The invasional meltdown hypothesis states that multiple invasive species introduced to a system may facilitate each other to enhance survival and/or spread, potentially yielding compound effects on the recipient system (Simberloff and Holle 1999). Yet, a large portion of invasive species research is conducted on a single species, with impacts measured only once (Crystal-Ornelas and Lockwood 2020). Similarly, increased disturbance (Bugnot et al. 2016, Uyà et al. 2018, Mahood and Balch 2019) and changing climate (Weiskopf et al. 2020) may enhance invasion success.

NEON-enabled science as a means to address questions of invasion impacts—Because of the coordinated monitoring approach that tracks plant and animal communities, soil and water conditions, microclimates, geomorphology, and carbon fluxes (among other measurements), NEON has the potential to study the holistic impacts of biological invasions on unprecedented scales. Detection of invasive species at NEON sites is informed by data products that catalogue species presence (plant presence and percent cover, phenology and Airborne Observation Platform imagery, landbird point counts, fish surveys, tick and mosquito sampling, and small mammal and ground beetle trapping), but there are dozens of additional data products relevant to the impacts of invasive species (Box 1; Appendix S1: Box S1). Early invasions in uncommon cover types at NEON sites may go undetected because plant survey plots are located only within a site's dominant cover types, but the frequent monitoring design will still provide valuable early detections of invasion within those dominant cover types. In areas where invasion has already occurred, NEON's time series data will help answer the question of the delayed impact of invasions on native diversity (Crystal-Ornelas and Lockwood 2020). Even in cases where there is relatively little change in the state of the invasion over the 30-yr period of the experiment, the pairing of yearly collection of plant community composition data with continuous climatic and net ecosystem exchange data will allow investigators to see how intra- and interannual climatic fluctuations affect intra- and interannual carbon fluxes, and how these relationships vary with different stages of invasion. It may be possible, for example, to (1) tease specific combinations of seasonal conditions that have the greatest effect on carbon cycling among invasion stages, (2) determine which processes are idiosyncratic to a particular system, and (3) determine whether there are broad generalizations that can be drawn across temperate ecosystems about how invasions affect the ability of

Box 1

A selection of NEON data products relevant for studying the impacts of terrestrial biological invasions. See Appendix S1: Box S1 for data products to identify invasion impacts on aquatic systems.

- Soil physical and chemical properties: distributed initial characterization (DP1.10008.001)
- Soil physical and chemical properties: Megapit (DP1.00096.001)
- Soil physical and chemical properties: distributed periodic (DP1.10086.001)
- Soil water content and water salinity (DP1.00094.001)
- Soil temperature (DP1.00041.001)
- Soil inorganic nitrogen pools and transformation (DP1.10080.001)
- Soil microbe community composition (DP1.10081.001)
- Root biomass and chemistry: Megapit (DP1.10066.001)
- Root biomass and chemistry, periodic (DP1.10067.001)
- Herbaceous clip harvest (DP1.10023.001)
- Woody plant vegetation structure (DP1.10098.001)
- Litterfall and fine woody debris production and chemistry (DP1.10033.001)
- Non-herbaceous perennial vegetation structure (DP1.10045.001)
- Phenology images (DP1.00033.001)
- fPAR—spectrometer—mosaic (DP3.30014.001)
- fPAR—spectrometer—flightline (DP2.30014.001)
- Site management and event reporting (DP1.10111.001)

ecosystems to cope with intra- and interannual climatic fluctuations.

Long-term planning or a better understanding of long-term impacts (costs and benefits) will allow for effective resource allocation in the short term. A recent case study in long-term management of invasive mammals (Mill et al. 2020) highlights five challenges that are just as applicable to the management of invasive plants: defining landscape-scale strategies, evidence requirements, sustainable funding, management coordination, and stakeholder engagement. The long-term commitment of NEON to collect multi-scale information across a national network can help address the first three of these challenges. Further coordination of NEON information to support management-relevant information could help with the final two.

Biological invasions do not occur in isolation, and understanding the interactions between multiple invaders, disturbance, and climate change will help inform a more holistic approach to invasive species management. By comparing well-defined impacts in systems across environmental gradients, we can progress toward evaluating management against both individual species and ecosystem-level responses. A network of consistent measurements across a range of species and at multiple scales can help address this question. Through this approach, invasive species risk assessment (Andersen et al. 2004) and related management actions in one ecosystem can inform actions in another while also highlighting how approaches might need to be customized for any given ecosystem.

CASE STUDIES

Here, we present case studies of how NEON data could be used to address these important questions in invasion biology. They are presented as useful illustrations of potential methods, rather than complete investigations, which could be expanded in order to provide more robust results with additional sites that are available, longer term data which will be produced over the lifetime of NEON, or additional parameters that are also being measured and reported. We focused our case studies on four terrestrial NEON sites that are located within the *Desert Southwest, Great Basin,* and *Southern Rockies & Colorado Plateau* eco-domains, a region with a history of profound change due to grass invasions (D'Antonio and Vitousek 1992, Fulbright et al. 2013). Sites included Onaqui and Moab in Utah, the Santa Rita Experimental Range in Arizona, and the Jornada Long-Term Ecological Research site in New Mexico (Table 2). Both Utah sites occur in a region with extensive spread of *B. tectorum,* while Jornada and Santa Rita are in a region with high levels of *E. lehmanniana* invasion (Fig. 1). Numerous other invasive plant species are of concern in each of these sub-regions of the Intermountain West.

Table 2. Study sites and attributes.

Site	Latitude (°N), Longitude (°E)	Elevation (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)
Jornada	32.59, −106.84	1329	17	173
Moab	38.25, −109.39	1767	11	200
Onaqui	40.18, −112.45	1685	9	388
Santa Rita	31.91, −110.84	983	20	290

We used the neonUtilities v. 1.3.8 package in R (Lunch et al. 2020, R Core Team 2020) to download and compile the data sets for the specified years and sites. The core data set for three of the case studies was the "Plant presence and percent cover" product (DP1.10058.001), which includes "Plant species presence as observed in multi-scale plots: species and associated percent cover at 1-m^2 and plant species presence at 10-m^2, 100-m^2 and 400-m^2" (Elmendorf et al. 2016). Surveys are conducted one or more times per year at all NEON sites to capture plant species cover in 1-m^2 nested plots, and species presence is recorded every other year in the larger nested plots. (Appendix S1: Fig. S1, reproduced from Barnett et al. 2019 with permission). Prior to 2019, species cover and presence were recorded concurrently once or more per year, but the protocol was changed to measuring six of the eight 1-m^2 subplots (omitting the two center subplots to avoid trampling) in every sampling bout, and measuring presence in the larger nested subplots only every other year (Elmendorf 2021). All code and data used in our analyses are available at https://github.com/admahood/six-invasion-questions.

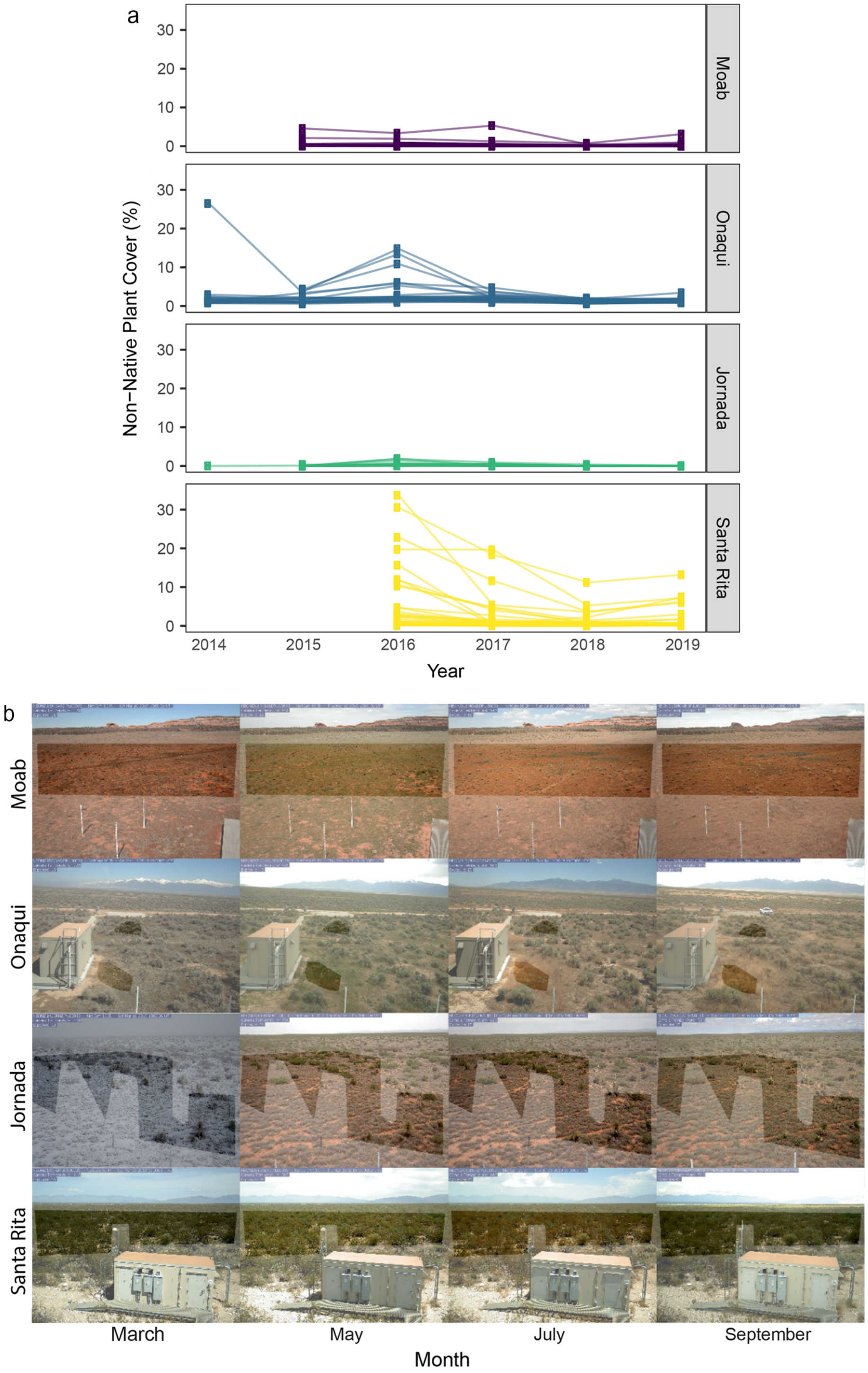

Fig. 1. (a) Non-native plant cover for each plot at each NEON site through time. Each line represents a different plot. (b) PhenoCam mid-day, mid-month images representing growing season months in 2019 (including snow at Jornada in mid-March). Masks represent the "region of interest" (ROI) from the PhenoCam Network which are used to extract daily estimates of greenness by plant functional type from digital repeat photography methods.

Case I: The relationship between native plant richness and non-native plant richness across scales

The relationship between the diversity of ecological communities and their invasibility by non-native species has been a topic of significant interest and discussion in community ecology. Numerous studies that focus on local scale interactions and dynamics have found a consistent pattern of locations with a greater number of native species being more resistant to invasion (often quantified as the number or abundance of non-native species; Kennedy et al. 2002, Fargione and Tilman 2005), supporting the Biotic Resistance Hypothesis. However, studies that consider diversity patterns at larger scales have found the opposite pattern, with native species richness and non-native species richness scaling together (Levine and D'Antonio 1999, Naeem et al. 2000). This scale-dependent shift in the direction of the relationship between native species richness and non-native species richness has been described as the "invasion paradox" (Fridley et al. 2007) and is likely driven by the combination of multiple processes including biotic resistance of diverse communities (Kennedy et al. 2002, Fargione and Tilman 2005), competitive exclusion by invasive species (Yurkonis et al. 2005, Muthukrishnan et al. 2018), and spatial heterogeneity providing a variety of habitats that support greater diversity (Davies et al. 2005).

Here, we used monitoring data from the four selected NEON sites (Jornada, Moab, Onaqui, and Santa Rita) to evaluate whether plant communities also displayed scale-dependent shifts in the relationship between native and non-native species richness. Additionally, by examining time series of community composition, we were able to test for biotic resistance as a specific mechanism driving the richness relationships. Taking advantage of the nested nature of the NEON sampling regime, we aggregated plant community composition from each site at four separate scales: 1 m^2, 10 m^2, 100 m^2, and 400 m^2. Plant diversity is sampled in numerous 400-m^2 plots at each site. Cover for each plant species was measured in eight 1-m^2 subplots, each of which is nested within one of eight 10-m^2 subplots where occurrence was recorded for any additional species not encountered in the 1-m^2 subplot. Pairs of the 10-m^2 subplots are each nested within one of four 100-m^2 subplots, where occurrence is recorded for any species not already encountered in the 1-m^2 and 10-m^2 subplots within (Appendix S1: Fig. S1, reproduced from Barnett et al. 2019 with permission). For each plot at each scale, we summed the number of native and non-native plant species present for each yearly time-step (Mahood 2020, Appendix S2).

We modeled invasibility using two approaches. We quantified the relationship between native species richness and non-native species richness using generalized linear models (GLMs) with a quasipoisson distribution due to overdispersion (Zuur et al. 2009), with a distinct model at each scale of the data (Table 3). We also estimated the probability that a plot was invaded (i.e., presence of at least one non-native species) as predicted by native species richness, using a binomial GLM. As observed in other systems, there was a scale-dependent shift in the relationship. We observed a negative relationship between native species richness and non-native species richness at the 1-m^2 scale and 10-m^2 scale and a positive relationship at coarser scales (Fig. 2a). Similarly, we found that native richness was negatively correlated with the probability of invasion in 1-m^2 plots, but when aggregating at broader scales, they were positively correlated (Fig. 2b, Table 3).

To look more specifically at evidence for biotic resistance, we used plots with repeated surveys to evaluate the influence of native species diversity on invasion in a subsequent time point. For this analysis, we identified locations that were uninvaded at any time point, the native species diversity at those locations, and whether the location was invaded in the following year, and if so, how many non-native species were present. We used GLMs (as above) to evaluate whether native species richness correlated with either non-native richness or the probability of being invaded in the following year. Here, the scale-dependent effect was less distinct and did not display a shift to a negative relationship at the finest spatial scales. However, while native species diversity had a positive relationship with non-native species richness (Fig. 2c) and probability of invasion (Fig. 2d) at all spatial scales, that effect was weaker at finer spatial scales and strengthened with the size of the sampling area. At the 1-m^2 and 10-m^2 scales, the probability of invasion did not rise above 50% nor did the

Table 3. Model coefficients (and standard errors) for GLMs evaluating the relationships between species diversity and invasion at different scales, with a different model for each scale.

Scale by Formula	Term	Estimate	SE	Statistic	*P*
Fig. 2a: non-native species richness ~ native species richness					
1 m^2	(Intercept)	0.70	0.035	20	<0.0001
	Native spp richness	−0.096	0.0064	−15	<0.0001
10 m^2	(Intercept)	0.66	0.031	21	<0.0001
	Native spp richness	−0.023	0.0031	−7.5	<0.0001
100 m^2	(Intercept)	0.71	0.035	21	<0.0001
	Native spp richness	0.0045	0.0018	2.5	0.012
400 m^2	(Intercept)	0.97	0.06	16	<0.0001
	Native spp richness	0.006	0.002	3.1	0.0021
Fig. 2b: *P*(invaded) ~ native species richness					
1 m^2	(Intercept)	0.18	0.057	3.2	0.0016
	Native spp richness	−0.042	0.0088	−4.8	<0.0001
10 m^2	(Intercept)	0.015	0.056	0.26	0.80
	Native spp richness	0.03	0.0053	5.6	<0.0001
100 m^2	(Intercept)	−0.17	0.08	−2.1	0.039
	Native spp richness	0.065	0.0053	12	<0.0001
400 m^2	(Intercept)	−0.16	0.19	−0.84	0.40
	Native spp richness	0.069	0.01	6.7	<0.0001
Fig. 2c: next non-native species richness ~ native species richness					
1 m^2	(Intercept)	−1.8	0.17	−11	<0.0001
	Native spp richness	0.031	0.023	1.3	0.18
10 m^2	(Intercept)	−1.8	0.15	−12	<0.0001
	Native spp richness	0.046	0.012	3.8	<0.0001
100 m^2	(Intercept)	−1.4	0.17	−8.3	<0.0001
	Native spp richness	0.054	0.0087	6.2	<0.0001
400 m^2	(Intercept)	−1.5	0.33	−4.6	<0.0001
	Native spp richness	0.074	0.013	5.8	<0.0001
Fig. 2d: *P*(next invaded) ~ native species richness					
1 m^2	(Intercept)	−2.2	0.16	−14	<0.0001
	Native spp richness	0.081	0.021	3.8	<0.0001
10 m^2	(Intercept)	−1.9	0.15	−12	<0.0001
	Native spp richness	0.053	0.013	4.1	<0.0001
100 m^2	(Intercept)	−1.8	0.21	−8.7	<0.0001
	Native spp richness	0.073	0.013	5.7	<0.0001
400 m^2	(Intercept)	−2.3	0.58	−4	<0.0001
	Native spp richness	0.11	0.032	3.4	<0.0001

Notes: Separate models used different metrics of invasion as response variables: the probability (*P*) of being invaded in the same year (Invaded) and the following year (Next Invaded) and non-native species richness in the same year (Non-Native Species Richness) and the following year (Next Non-Native Species Richness). Models with probability of being invaded as the response use a "binomial" error distribution and those with non-native species richness use a "quasipoisson" error distribution.

predicted number of non-native species rise above 1, which suggests that even though the relationship with native species richness is positive, samples are more likely to remain uninvaded than be invaded. The positive relationship when evaluating changes from one year to the next suggests biotic resistance is weak within these systems and that the general relationship between native and non-native species richness is likely driven by other mechanisms such as habitat quality or heterogeneity (e.g., Muthukrishnan et al. 2018).

Case II: Landscape features as predictors of biological invasions

The spatial patterns of landscape features (e.g., transportation corridors and barriers) may promote invasion through different mechanisms,

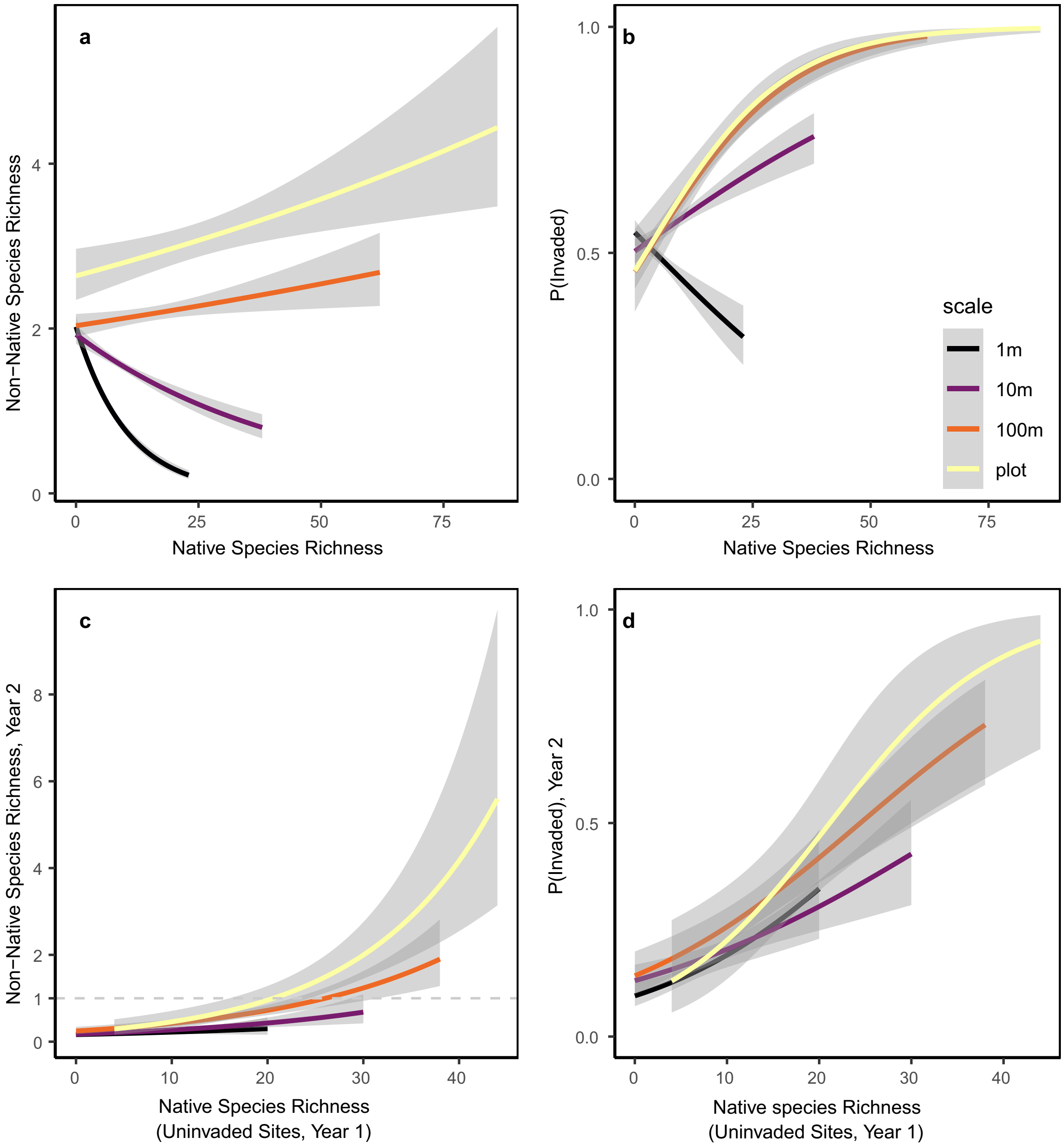

Fig. 2. Using plant community data from four NEON sites we quantified the relationship between native species richness at a given location and (a) the number of non-native species present or (b) the probability that at least one non-native species was present. Additionally, we aggregated data at different spatial scales (lines of different colors) to evaluate whether these relationships are scale-dependent. We also evaluated biotic resistance in those locations (and at different spatial scales) by quantifying the relationship between native species richness at locations with no non-native species and (c) the number of non-native species present in the following year or (d) the probability that at least one non-native species was present in the following year.

such as their influence on human populations and propagule pressure (McKinney 2006, Simberloff 2009, Moles et al. 2012). Propagule pressure, or the number of dispersal events and propagules per event (Lockwood et al. 2005), is a critical attribute in determining the success of an invasion. Increased introduction attempts enhance the likelihood of non-native species becoming established, and therefore, invasiveness increases as the number of dispersal events rises (Pyšek et al. 2009). Because direct measurement of propagule pressure is difficult, measurements of landscape structure, composition, and complexity (Vicente et al. 2019), distance to potential sources such as gardens (Conedera et al. 2018), botanical gardens (Dawson et al. 2008), and roads (Warren et al. 2019) may be adopted as proxies. In addition, common landscape features associated with the transportation network including roads, trails, rail lines, and power line corridors are often linked with the spread of invasive plants (Gavier-Pizarro et al. 2010, Vilà and Ibáñez 2011, Fusco et al. 2016).

Therefore, as an example of how NEON data could be used to address these issues, we explored the proximity of the nearest road and native species richness as predictors of the abundance and cover of non-native plant species at the 20 m × 20 m plot level at the four selected NEON sites: Jornada, Moab, Onaqui, and Santa Rita. This size is the standard NEON plot size and thus is the natural scale for aligning plant community sampling data with other abiotic monitoring data. NEON established plots of this size to capture species across a diversity of systems with replication within each site (Barnett et al. 2019). NEON plant presence data are recorded by species in numerous 400-m^2 plots at each site one or more times per year (Appendix S1: Fig. S1, reproduced from Barnett et al. 2019 with permission). We predicted that the richness and cover of non-native species would decrease with increased distance to the nearest road. Native species richness was included as a predictor in the model as a proxy for habitat quality, as resident communities respond locally to biotic interactions within and across species along with environmental conditions. The distance from each plot to the nearest road was calculated using road data from various sources (Appendix S1: Table S3) and R package *'sf'* (Pebesma 2018). The model was fit using the package *"lme4"* and function *"glmer"* (Bates et al. 2015). Summary statistics for the plot distance to nearest road by site are given in Appendix S1: Table S4.

Contrary to our expectations, incorporating distance to the nearest road as a factor driving non-native species richness did not improve the strength of the model beyond that of the model that included only native species richness. The strongest models for predicting non-native species richness included native species richness alone and both distance to the nearest road and native species richness as predictors (Fig. 3; Table 4). The single strongest model included native species alone as a unique predictor of the richness of non-native plant species, although the strength of this model was very similar to models that included distance to the nearest road as an additional significant factor. Distance to roads alone was not a significant predictor of non-native species richness. For non-native species cover, none of the models exhibited strong predictive power (Table 4), suggesting that other factors that were not considered are driving the total percent cover of non-native plants, a variety of which can still be explored using additional NEON products and other data. Additionally, because early invasion dynamics are highly stochastic, as the length of NEON data sets grow and if invasive species expand or establish in additional locations, it may become easier to identify a signal of the influence of roads on invasion dynamics.

Comparing results between sites, we found distance to the nearest road (as a proxy for propagule pressure and anthropogenic disturbance) to be a more important driver of invasion in Onaqui and Jornada sites, which supported our prediction that invasive species cover would be highest near roads. For unknown reasons, non-native species richness at Moab and Santa Rita followed opposite trends, increasing with greater distance from roads. Further analysis should account for intrinsic characteristics of the sites as well as additional landscape features in order to improve the accuracy of these predictions (Moles et al. 2012).

Case III: Total soil nitrogen and invasion

Nitrogen availability tends to be low in drylands due to low organic material, but N deposition is increasing across the American West due

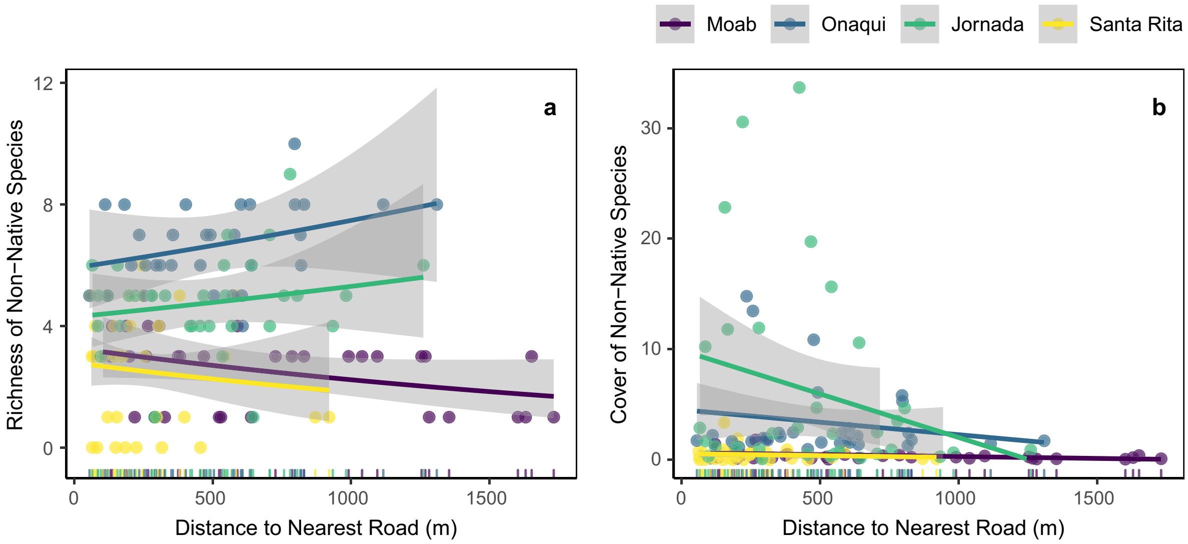

Fig. 3. Richness (number of non-native plant species per plot) and cover (plot-level averages) of non-native plants as a function of distance to the nearest road at four NEON sites (point and line colors indicate different sites: Onaqui, Moab, Santa Rita, and Jornada) in 2016. Trend lines and shaded areas indicate mean predictions and 95% confidence intervals from a generalized linear model based on a Poisson distribution (a) and a normal distribution (b). The data points are derived from the raw cover data collected by NEON. The rug on the bottom of the graph shows the individual plot distances to the nearest road (in the corresponding site colors), jittered to distinguish different data entries.

Table 4. Results for the different generalized linear mixed models tested to predict non-native species richness and cover in Case Study II.

	Incidence rate ratios (CI) by predictor variable				
Formula	Native richness (NR)	Distance to road (DR)	NR × DR	Marginal R^2	AIC
Non-native richness ~ native richness	1.64*** (1.25–2.17)	N/A	N/A	0.220	502.791
Non-native richness ~ distance to road	N/A	1.05 (0.74–1.49)	N/A	0.003	517.155
Non-native richness ~ native richness + distance to road	1.64*** (1.25–2.16)	1.02 (0.71–1.47)	N/A	0.219	504.77
Non-native richness ~ native richness × distance to road	1.65*** (1.25–2.17)	1.02 (0.69–1.49)	1.03 (0.54–1.96)	0.219	506.771
Non-native % cover ~ native richness × distance to road	−0.69 (−3.42–2.03)	−0.97 (−3.76–1.82)	0.98 (−4.49–6.46)	0.015	781.82
Non-native % cover ~ native richness + distance to road	−0.65 (−3.35–2.06)	−0.93 (−3.68–1.82)	N/A	0.012	783.192
Non-native % cover ~ distance to road	N/A	−1.04 (−3.73–1.65)	N/A	0.009	783.830
Non-native % cover ~ native richness	−0.77 (−3.47–1.93)	N/A	N/A	0.005	784.136

Notes: The models tested different hypotheses in predicting the number of invasive species using Akaike's information criterion (AIC) through the package "*bbmle*" and function "AICtab" (Bolker and R Core Team 2020). Distance from the plot to the nearest road and the number of natives species per plot were centered and standardized. All statistical tests were performed in R (R Core Team 2020).

*** $P < 0.001$.

to anthropogenic activities (Fenn et al. 2003), with a variety of impacts on community composition including the facilitation of biological invasions (Pardo et al. 2011). Nitrogen availability is both a driver of and response to increased invasive species biomass; high resource availability can favor invasive species (Vasquez et al. 2008), and invasive plants can change decomposition to affect available N (Parker and Schimel 2010, Perry et al. 2010). Here, we investigate how total soil N concentration and N deposition (as proxy metrics of N availability) correlate with invasive plant cover across the Moab, Santa Rita, Jornada, and Onaqui NEON sites. To understand invasions at both site and regional scales, N stocks and fluxes are key resources to track.

We used the "Soil chemical properties" data product that reports %C and %N in the top 30 cm of soil and the "Plant presence and percent cover" data product. In each 20 m × 20 m plot, we evaluated the relationship between total soil N (%) and average cover of non-native plants in 2016 with linear models, including site and total soil N as predictors of non-native plant cover, averaged to the 20 m × 20 m scale. Plant percent cover by species is recorded in multiple 1 m × 1 m plots nested within each 20 m × 20 m at all NEON sites at least one time per year (Appendix S1: Fig. S1, reproduced from Barnett et al. 2019 with permission). At the site level, we also extracted N deposition values from spatially explicit N deposition models (Holland et al. 2004) for the locations of the NEON sites. We then evaluated average cover of non-native plants by year from 2014 to 2018 as a function of N deposition using linear mixed effects models (Bates et al. 2015) with site and total N as main effects and year as a random effect.

We found that at the plot level, there was generally higher cover of non-native species than native species and a positive relationship between non-native species cover and total soil N concentration at Santa Rita (post hoc slope = 27.49 ± 8.20 [mean ± SE]) compared with other sites; Jornada, Moab, and Onaqui did not have relationships with total soil N that were significantly different than zero (site: $F_{3,27} = 6.54$, $P = 0.002$; total soil % N: $F_{3,27} = 2.64$, $P = 0.116$; total soil % N × site: $F_{3,27} = 4.98$, $P = 0.008$; Fig. 4a). At the site level, we did not find any relationships between non-native cover and N deposition (N deposition: $F = 0.10$, $P = 0.927$, site: $F = 1.34$, $P = 0.33$). Together, we can begin to make predictions that in a site-like Jornada with low current invasive cover and soil N (Fig. 4a) but relatively high N addition potential through deposition (Fig. 4b), we may begin to see strong responses to microsite variability in N, as we observed in Santa Rita.

Within-site variance in total soil N concentration was more indicative of non-native plant cover than regional differences in anthropogenic forcing of resource availability (i.e., site). As abundance and cover of non-native species fluctuate over time, these changes can be compared against changes in total soil N (which are observed at five-year intervals through NEON; Soil N Transformations data product), potentially shedding light on whether N availability serves as driver or effect of grass invasion. The result that site differences are more important than within-site variability supports the notion that N is relatively fleeting and can change more rapidly, thus making larger differences by site more important. Similar analyses can also be conducted with other environmental parameters to test whether other factors may be better predictors of invasions in these systems.

Case IV: Phenology data distinguish Bromus tectorum *L. from native vegetation and allow for enhanced monitoring of spread*

Monitoring the progression of biological invasions through different stages is a challenge because consistent, repeated observations are needed across large areas. Remote-sensing imagery may provide a method for frequent monitoring of dynamics over a broad area, but distinguishing species at the scale of such imagery is often very difficult, especially for invasive understory species (Huang and Asner 2009). However, near-surface imagery taken from the ground or canopy level may provide an opportunity to characterize temporal patterns that can be used to distinguish species via frequent image capture yielding differences in their phenology (Huang and Asner 2009). As a part of NEON Terrestrial Instrument System data collection, two phenological cameras (PhenoCams) mounted on towers at each site use digital repeat photography methods to capture understory and canopy-level greenness indices. These cameras use "regions of interest" (ROIs) to extract phenological signals such as time series of relative greenness (greenness chromatic coordinate, GCC) and key transition thresholds such as greenness onset or senescence (Richardson et al. 2018, Seyednasrollah et al. 2019, Fig. 1b). Thus,

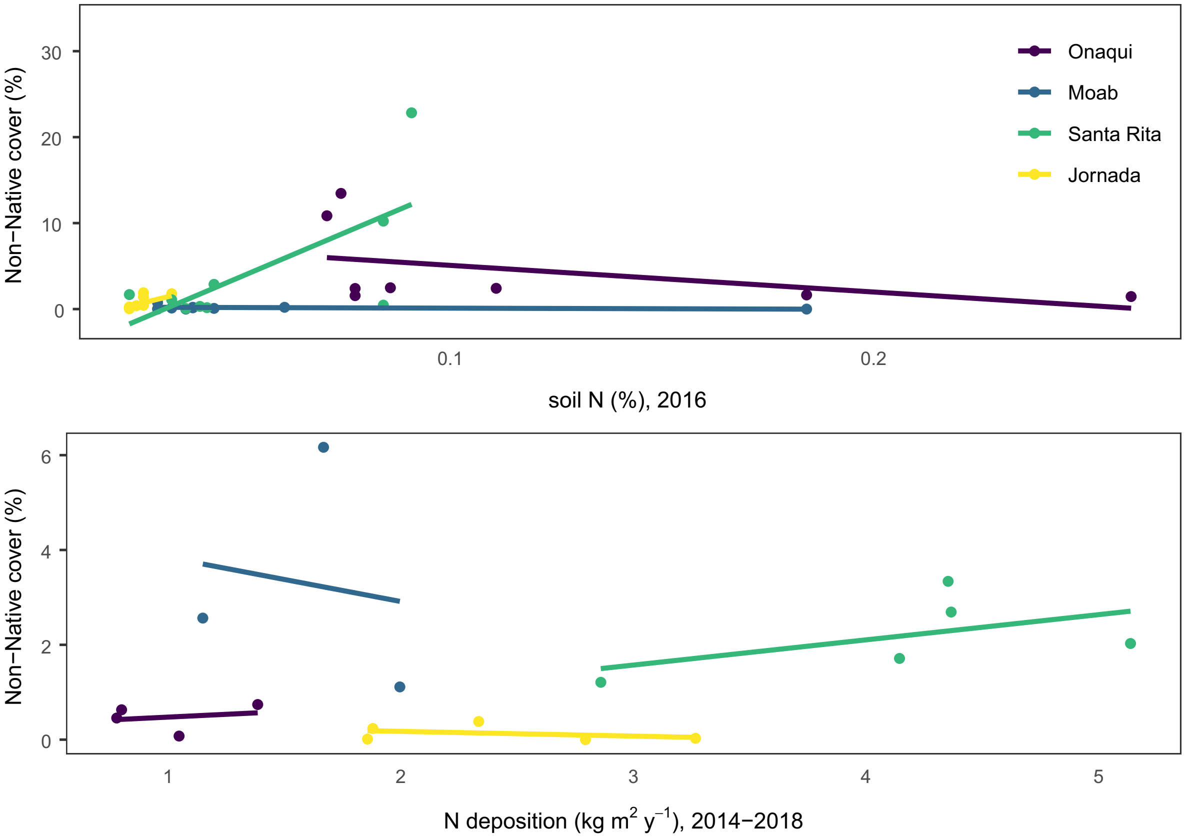

Fig. 4. Non-native grass cover as related to soil N concentration and N deposition. Average non-native grass cover (%) and total soil N (%) by 20 × 20 m plot at four NEON sites in 2016 (top row) and mean non-native grass cover (%) and total N deposition (kg·m^{-2}·yr^{-1}) averaged to site level from 2014 to 2018 (bottom row).

the unique phenological strategies of some invasive species, such as advanced greenup and browndown of *B. tectorum*, position PhenoCams well to capture the progression of biological invasions, effectively distinguishing them from native plants at a high level of precision while also tracking their spread and abundance at frequent intervals. Recent improvements in PhenoCam ROIs at the Onaqui NEON site have allowed for the extraction of *B. tectorum* phenological signals versus native shrubs, which are in agreement with in situ phenology observations of leaf development from NEON's Terrestrial Observation System field campaigns (Fig. 5).

Bromus tectorum is known to exist at additional NEON sites including Moab, UT (arid shrub/herbaceous), Klemme Range Research Station, OK (grassland), San Joaquin Experimental Range, CA (open woodland/herbaceous), and Soaproot Saddle, CA (evergreen forest). Automated scripts have been developed to look for unique patterns in greenup and browndown of *B. tectorum* in NEON PhenoCam greenness signals (e.g., GCC). This could allow for the early and frequent detection of changes in *B. tectorum* cover at these sites, enabling rapid management of an invasion (Fig. 5). Further, multiple NEON Airborne Observation Platform campaign flights over the course of the phenological phase of *B. tectorum* could detect its extent and expansion. Integrating in situ (NEON Terrestrial Observation System), near-surface remote sensing (NEON Terrestrial Instrument System PhenoCam), and remotely sensed data (NEON Airborne Observation Platform) could improve our detection of invasion events by plants such as *B. tectorum*, along with

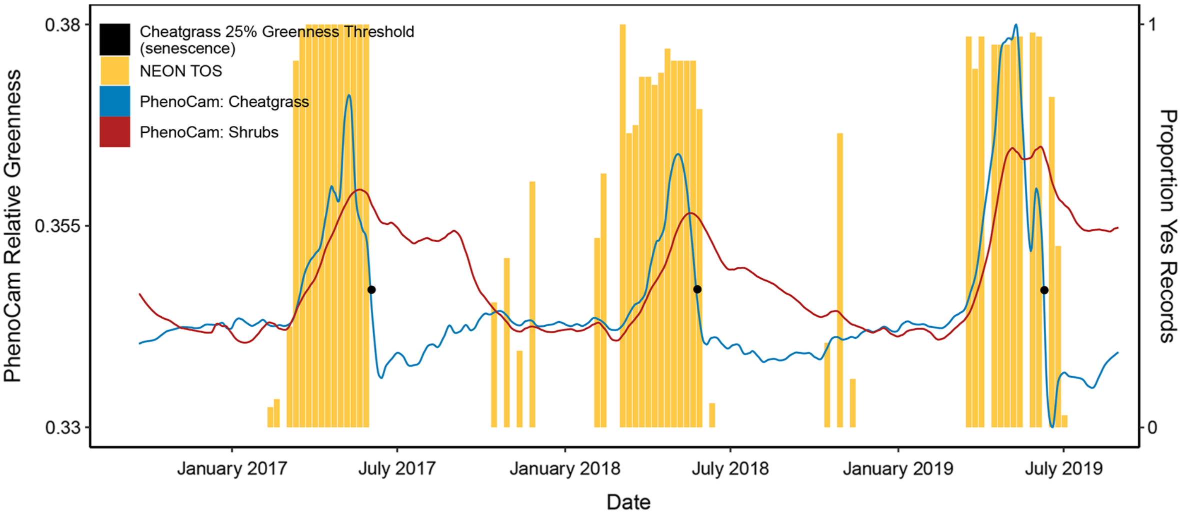

Fig. 5. Agreement in phenology data for *Bromus tectorum* at NEON's Onaqui site among the PhenoCam-derived estimates of vegetation greenness and in situ observations (NEON Terrestrial Observation System; TOS) at NEON's Onaqui site for invasive *Bromus tectorum* (blue) versus native shrubs (red). Vertical bars represent in situ observations of green leaves for *B. tectorum*. Differentiating the rapid browndown of invasive *B. tectorum* (blue) relative to native shrubs (red) could aid in the detection of *B. tectorum* invasions, and timed NEON Airborne Observation Platform flights at key thresholds such as 25% greenness could improve estimates regarding the spatial extent of invasions.

their extent at landscape-to-continental scales (Landsat, MODIS).

SYNTHESIS

Outstanding questions about the ecology of biological invasions are complex, and while the NEON endeavor is by no means a panacea for addressing these questions, there are many novel elements in its structure that make it uniquely poised to contribute to addressing some of these questions. Here, we showed a proof of concept, highlighting a few opportunities that NEON data offer for investigating questions of drivers of invasion, and demonstrating their implementation. Other NEON data can be explored as incorporating metrics of abundance and the spatially nested nature of the plots. Furthermore, NEON sites were selected to represent different ecosystems and vegetation types in the United States, and NEON data products therefore provide the opportunity to investigate multiple landscape effects on the likelihood of invasion, impacts, and new invasions, both across sites and using repeated sampling over time within sites. These four case studies demonstrate how advancements in this regard can be made incrementally with relatively simple analyses of NEON data, potentially leading to broader-scale syntheses and application for management. Case Study I offers an example of how the nested nature of NEON sampling might be used to test how ecological relationships vary with spatial scale. This is known to be particularly relevant to questions of biotic resistance, as we have focused our attention here, but can also be a useful tool for evaluating ecological relationships over multiple scales generally. In Case Studies II and III, we brought in ancillary data to determine how well and how consistently the richness and percent cover of non-native plants could be predicted from proximity to roads and soil nutrients, two factors that are often associated with the spread of invasive species (Cherwin et al. 2009, Joly et al. 2011). Case Study IV demonstrates how tracking the unique phenological signals of some invasive species can improve our detection of invasions and track their progression, potentially through different stages. This method could be applicable to other species and regions. Overall, these case studies shed light on the fact that native plant diversity is an important, yet scale-sensitive, predictor of plant invasions compared with other factors in the Desert Southwest and Southern Rockies and Colorado Plateau, and that understanding variance across spatial and temporal scales is highly important in predicting the relative abundance of important invasive plants in this region.

Applications for management

The long-term and continental-scale aspects of NEON data provide an opportunity to make data-driven management decisions. Establishing the network has relied on close communication with land management partners. Of the 81 NEON sites (47 terrestrial and 34 aquatic), over half are on lands managed by federal agencies, while other sites are managed by states, non-government organizations (NGOs), and universities. The mission of the Jornada Experimental Range is to conduct science that addresses problems confronting the conservation and management of arid lands in the United States, North America, and around the world. The Santa Rita site is hosted by the University of Arizona, where the site serves to advance research and education on the ecology and management of desert rangelands. The Onaqui and Moab sites are on property administered by the U.S. Bureau of Land Management (BLM), managed in accordance with the Federal Land Policy and Management Act. These sites were chosen as nationally representative locations for ecological studies. Motivations for work at these sites that pre-date NEON include concerns on how ecological insight can be used to inform proper management of ecosystems represented by that site. Information regarding management actions in NEON sites and individual plots can be accessed through NEON's Site Management and Event Reporting data product (DP1.10111.001). The sites used in the case studies presented here are reflective of that joint ecological and land management nexus.

As land management concerns are critical at each site and as invasive species pose significant management challenges (Crowl et al 2008), the questions and case studies presented here highlight the relevance of NEON data to inform both ecology and management issues. Whether it is reducing the risk of wildland fire or promoting sustainable grazing practices, prediction of biological invasions (Buckley and Catford 2016) and understanding the impacts of invasive species on recipient systems (Sutherland et al. 2013) can help inform land management actions. Management actions are often resource constrained. Prioritizing actions to locations with the highest preventable risk of invasion or potential impacts can maximize limited resources. Knowing the potential impacts from invasive species can help prioritize invasive species actions among other actions competing for resources. To the extent that NEON data can inform invasion biology within an ecological domain, it can also inform land management actions in that domain.

Best practices for first-time NEON data scientists

Familiarize—We urge first-time NEON data users to take the time necessary to become familiar with the data products before using them to study biological invasions. Many ecologists have been trained to collect data by spending extensive time in the field, developing a familiarity for our study system in the process. The fact that NEON-enabled science removes that task for end users presents both an opportunity and a challenge. Numerous resources are available through the NEON Science Learning Hub (www.neonscience.org/resources/learning-hub), including informational videos, tutorials for using NEON products and practicing data science skills, teaching modules and professional development opportunities for educators, and information on upcoming workshops. Developing a familiarity with the suite of data products that are available, the nature of the data themselves, and the site characteristics can help to overcome the challenges of being unfamiliar with the data collection process.

We identified several key points for researchers to understand when it comes to using NEON data to address questions related to invasive species. First, the recent release of the NEON "Site management and event reporting" data product will provide site-level insight into important factors that affect invasive species moving forward, including grazing, spraying, invasive management, flood, and fire, and studies aiming to consider detailed (or pre-NEON) site history and management should integrate other data as needed. Second, the native status field within the NEON "Plant presence and percent cover" product has many (0–28%, mean 13% within the years and sites we evaluated, Appendix S1: Table S5) species' native status codes marked as unknown. This is often due to uncertainty in species identification. This can be updated by reviewing the local flora and consulting with local experts, including NEON botanists. Even if the specific epithet is uncertain, the biogeographic origin of some taxa can be determined simply by confirming that no species of that genus or family are native (or non-native) to a region. Finally, at NEON terrestrial sites, plant diversity plots are allocated across the landscape only into those National Land-Cover Database (NLCD) vegetation types that comprise >5% of the total area of the site. As such, the NEON sampling design may not detect the beginning of a species invasion at terrestrial sites if invasion begins within microsites in less dominant NLCD vegetation types that are not sampled. In this context, NEON data from dominant NLCD vegetation types provide a robust baseline from which to understand invasion progress, and there is an opportunity for PIs to build upon NEON data by collecting targeted data from more rare vegetation types in order to understand the dynamics of early invasion.

Familiarity with the suite of NEON products available will help researchers push the field of invasion ecology forward. However, familiarization must not stop there. Bringing together multiple NEON data products is powerful but requires an intricate knowledge of each product's sampling design and spatial and temporal resolution. A user must understand how data for some products may have been sampled in multiple bouts per year at one site but only in a single bout at another site, depending on the phenology of local plant communities. The nested-scale nature of the plant diversity data makes them ideal for addressing some of the most important questions facing the field of invasion biology, but also introduce complexity to data processing. The site management and event reporting data product should always be examined, and site descriptions should be reviewed along with previously published research from the site(s). This is particularly important with respect to understanding disturbance, management, and invasion history prior to the beginning of NEON data collection.

Collaborate—NEON data present the opportunity to gain a holistic perspective of ecosystems and their vulnerability and response to invasion, but no single researcher will have the expertise to leverage all 181 data products. Collaboration across sub-disciplines of ecology will allow this holistic perspective to unfold. Furthermore, collaboration with experts outside of ecology, such as data scientists, social scientists, computational researchers, and engineers, will lead to novel understanding across disciplines. Finally, we suggest users collaborate with NEON site managers and staff scientists to help fill knowledge gaps that arise from analyzing data without involvement in sampling design or having been on site for their collection.

Integrate—There are numerous NEON data products that may inform biological invasion studies, but even more untapped potential exists in the integration of these products with other information. The first steps in integrating some NEON data products with other resources are already in place. For example, NEON PhenoCams align with and are available as part of the broader PhenoCam Network (Richardson et al. 2018, Seyednasrollah et al. 2019). Similarly, eddy-covariance data are readily integrated with the global FluxNet (Roy et al. 2016); for example, NEON eddy-covariance data are published and served via AmeriFlux as well as the NEON Data Portal. When NEON data are downloaded via the AmeriFlux portal, metadata, gap-filling, and file formats are standardized and the data sets are fully interoperable. NEON eddy-covariance data will also be included in the global FluxNet at the next data release from that network (Metzger et al. 2019). In our second and third case studies, we demonstrated how integrating spatial data representing roads and soil N concentration and N deposition allowed us to examine drivers of plant invasions in a way that cannot be done with NEON data alone. While we give only a few examples here, the possibilities to integrate with other local, regional, national, and global data sets are innumerable. This again highlights the importance of our second piece of advice—collaborate. Collaboration will connect users of varying research backgrounds who have familiarity with different external data sets.

Start small—How does one eat an elephant? One bite at a time. It is not possible to address any of the six questions that we have highlighted in this review with a single study. Rather, the ecological research community will make progress one nibble at a time. The same can be said for many other pressing questions in invasion biology. NEON data are a metaphorical elephant in their own right. Thus, a word of advice we offer is to focus on important, tractable questions that can be answered with available data. For example, we focused these case studies on questions of the mechanisms behind terrestrial plant invasions in the Desert Southwest, Colorado Plateau, and Southern Rockies. From here, additional steps can be taken to scale out similar questions to a national level, to integrate additional NEON and external data products, and to expand analyses to include other taxa. This pattern of using Big Data to address important components of big questions will help advance the field of invasion biology.

Share—Our final word of advice is to be assertive in sharing reproducible research methods, analytical code, and results. The NEON project is built upon the concepts of open science, and its utility and impact will continue to grow as users continue to share information through open-source code, publicly archived data, and open-access publications. Sharing should make data "Findable, Accessible, Interoperable, and Reusable" (FAIR; Wilkinson et al. 2016). Sharing data in an archive is important, but data are more reusable if they contain descriptive metadata and are archived in a non-proprietary format (Poisot et al. 2019). Doing so will again feedback to the process of collaboration, yielding massive benefits to invasion biology and pushing researchers toward discovering new horizons in the discipline.

CONCLUSIONS

Our case studies have demonstrated how we can incrementally address important questions about the mechanisms (Topic 1) of biological invasions. Over time, the ability of NEON data to address the impacts of invasions (Topic 2) will strengthen, eventually including multi-decadal impacts. Given the spatial and temporal scale of NEON data and the numerous data products, there is a rich opportunity to observe invasions and identify associated changes in microbial, plant, and invertebrate communities, carbon fluxes, and other biogeochemical cycles. Finding strong relationships is the first step to identifying underlying mechanisms (Meyerson et al. 2019), and NEON is currently well-poised to uncover those trends. Further, with multiple types of monitoring, including monitoring quadrats and collecting PhenoCam and airborne remotely sensed data, we can begin to assess changes at fine spatial and temporal resolutions, ultimately improving the ability to forecast changes in invasive species through time.

For local, regional, and even global-scale land managers and policymakers, the data collected by NEON will be instrumental in decisions for on-the-ground activities. One key feature of continuous monitoring is the potential for early detection of an invasion (a key component of a national invasive species information network; Reaser et al. 2020) when targeted activities may keep it from spreading. One benefit of broad-scale data across multiple environmental gradients is being able to understand where invasive species are likely to spread (Analysis step, Stohlgren and Schnase 2006). Managers can then allocate resources to the areas most likely to be affected, or the areas where intervention will have the strongest impact. Understanding invasion impacts (Stohlgren and Schnase 2006) will allow land managers to decide which species must be prioritized for control given limited resources and potentially multiple simultaneous invasions.

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DATA AVAILABILITY

All code and data used in the analyses are available from Zenodo: https://doi.org/10.5281/zenodo.4705449

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3728/full