Influence of the Allee effect on extreme events in coupled three-species systems

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MS received 27 September 2021; accepted 15 February 2022

We considered the dynamics of two coupled three-species population patches by incorporating the Allee effect and focused on the onset of extreme events in the coupled system. First, we showed that the interplay between coupling and the Allee effect may change the nature of the dynamics, with regular periodic dynamics becoming chaotic in a range of Allee parameters and coupling strengths. Further, the growth in the vegetation population displays an explosive blow-up beyond a critical value of the coupling strength and Allee parameter. Most interestingly, we observed that beyond a threshold of the Allee parameter and coupling strength, the population densities of all three species exhibit a non-zero probability of yielding extreme events. The emergence of extreme events in the predator populations in the patches is the most prevalent, and the probability of obtaining large deviations in the predator populations is not affected significantly by either the coupling strength or the Allee effect. In the absence of the Allee effect, the prey population in the coupled system exhibits no extreme events for low coupling strengths, but yields a sharp increase in extreme events after a critical value of the coupling strength. The vegetation population in the patches displays a small finite probability of extreme events for strong enough coupling, only in the presence of the Allee effect. Last, we considered the influence of additive noise on the continued prevalence of extreme events. Very significantly, we found that noise suppresses the unbounded vegetation growth that was induced by a combination of the Allee effect and coupling. Further, we demonstrated that noise mitigates extreme events in all three populations, and beyond a noise level, we do not observe any extreme events in the system. This finding has important bearings on the potential observability of extreme events in natural and laboratory systems.

Keywords. Allee effect; coupled nonlinear systems; extreme events; population dynamics

1. Introduction

Investigating the advent of extreme events which signal behaviour beyond normal variability in the dynamics of complex systems has enormous relevance from the viewpoint of basic understanding of complex systems, as well as implications for risk assessments from catastrophic surges (Strogatz 2003; Kinney et al. 2005; Solli et al. 2007; Lubchenco and Karl 2012). So, exploring the emergence of such events in models and real-world systems, as well as the search for mechanisms and processes that may underlie extreme events, has witnessed much research interest in recent years (Albeverio et al. 2006). An extreme event can be labelled as one where a state variable displays very large, relatively rare fluctuations from the average value. That is, in the course of its evolution, the system exhibits occasional uncorrelated excursions that are significantly different from the mean. So, the most commonly employed signature of extreme events in phenomena ranging from oceanography (Dysthe et al. 2008) to financial markets (Lillo and Mantegna 2003) is uncorrelated recurrent deviations larger than a

This article is part of the Topical Collection: Emergent dynamics of biological networks.

http://www.ias.ac.in/jbiosci
Published online: 19 May 2022
prescribed threshold of typically 3–8 standard deviations away from the average value.

A very important direction in the study of extreme events is to unearth generic mechanisms that can give rise to such large deviations in the dynamics. While extreme events in stochastic models have been extensively studied over decades (Majumdar and Ziff 2008; Kishore et al. 2011), the advent of extreme events in deterministic dynamical systems, without intrinsic or extrinsic stochasticity, has garnered focus only in recent times (Balakrishnan et al. 1995; Ansmann et al. 2013; Karnatak et al. 2014; Kingston et al. 2017; Moitra and Sinha 2019; Chaurasia et al. 2020).

Focussing on this, we considered the emergent extreme phenomena in patches of vegetation–prey–predator systems coupled through the Lotka–Volterra interactions, incorporating the biologically important Allee effect. In population dynamics, the Allee effect reflects the advantageous influence of conspecific interactions on population growth (Dennis 1989; Courchamp et al. 2008; Sen et al. 2021) and captures the impact of small population size on the long-term persistence of a population. Further, we considered the role of noise on the propensity of extreme events in this coupled three-species system. Beyond modelling population dynamics in ecosystems, these results have broad bearings on the mechanisms that can enhance extreme events in deterministic dynamical systems, and the effect of stochasticity on their prevalence.

Our article is organized as follows: At the outset, in section 2 we introduce the model of three interacting species, incorporating the Allee effect, and recall some significant results in this system. In section 3 we go on to explore the dynamics of coupled patches of such three-species systems to establish the generality and broad scope of our findings. Lastly, in section 4, we summarize our results and discuss their potential implications.

2. Three-species food chain model with the Allee effect

The local and global dynamics of three-species interacting models have significant impact on complex systems research, in particular in theoretical ecology. Here we considered a vertical food chain model incorporating the dynamics of the snowshoe hare and the Canadian lynx populations, based on observed data. This model consists of vegetation (denoted by \( u \)), prey (denoted by \( v \)) and predator (denoted by \( w \)), and also incorporates the Allee effect into the growth of the predator populations. The dynamics of the model can be described by the following coupled nonlinear ordinary differential equations:

\[
\begin{align*}
\dot{u} &= f(u, v, w) = au - \alpha_1 f_1(u, v), \\
\dot{v} &= g(u, v, w) = \alpha_1 f_1(u, v) A(v) - bv - \alpha_2 f_2(v, w), \\
\dot{w} &= h(u, v, w) = \alpha_2 f_2(v, w) - c(w - w^*)
\end{align*}
\]

where \( a, b \) and \( c \) are the growth rates of vegetation, prey and predator populations, respectively. Here the interaction between vegetation and prey was considered to follow the Holling type II functional response \( f_1(u, v) = \frac{uv}{1+ku} \), whereas the interaction between prey and predator was considered to follow the Lotka–Volterra type interaction, described by \( f_2(u, v) = uv \). The parameter \( k \) corresponds to the average time spent for processing a food item, and is termed “handling time” (Metz and Diekmann 1986). Here \( \alpha_1 \) denotes the maximum growth rate of the prey, which is the product of the ingestion rate and a constant factor less than unity, considering the fact that not all ingested vegetation population is converted into prey biomass. The parameter \( \alpha_2 \) corresponds to \( \alpha_1 \) in the predator population. The predator is considered to be a generalist, accounting for the fact that it can persist at an equilibrium \( w^* \), either in the absence of prey or when its concentration is low. Additionally, we incorporate the Allee effect into the prey’s growth by introducing the following functional form:

\[
A(v) = \frac{v}{v + \theta}
\]

where \( \theta \) is the Allee parameter reflecting the critical prey density at which the probability of successful mating would be half. This form is characteristic of the fact that the per-capita reproduction rate becomes smaller at low prey density. This kind of Allee effect appears due to lack of mating partners, low fertilization efficiency, cooperative breeding mechanism, etc., in the context of biology. The dynamics of this three-species model and the consequences of the Allee effect on this system has been very recently studied by Sen and Sinha (2021). We recall the principal results from that study below:

(i) The Allee effect induces an explosive increase (which we term a “blow-up”) of the vegetation population, i.e. there is a critical threshold of the Allee parameter beyond which the vegetation population has a positive probability of unbounded growth.
(ii) While this three-species system is regular when the Allee effect is absent or small, a sufficiently large Allee effect induces chaos in the system.

(iii) The Allee effect also has an impact on the development of extreme events in the three-species system, with the Allee effect typically enhancing the probability of obtaining such events.

(iv) Lastly, additive noise in this three-species system mitigates the blow-up of the vegetation population, and suppresses extreme events.

3. Patches of three-species systems coupled through cross-predation

In order to gauge the generality of the phenomena observed in a single patch in our earlier work, we now explore the dynamics of two coupled patches, where each patch again has three species, namely, vegetation, prey and predator. The populations in local patches are connected in such a way that the predator of one patch can attack the prey of neighbouring patches, and vice versa. This coupling strategy, known as coupling through cross-predation, signifies that predators are more mobile compared to prey and can move into another patch to capture the prey. The dynamics of the coupled three-species system can be described by the following set of equations:

\[
\begin{align*}
\dot{u}_1 &= f(u_1, v_1, w_1), \\
\dot{v}_1 &= g(u_1, v_1, w_1) - C v_1 w_2, \\
\dot{w}_1 &= h(u_1, v_1, w_1) + C v_2 w_1, \\
\dot{u}_2 &= f(u_2, v_2, w_2), \\
\dot{v}_2 &= g(u_2, v_2, w_2) - C v_2 w_1, \\
\dot{w}_2 &= h(u_2, v_2, w_2) + C v_1 w_2
\end{align*}
\] (2)

Here the populations of vegetation, prey and predator in the \(i\)-th patch \((i = 1, 2)\) are denoted by \(u_i, v_i\) and \(w_i\), respectively, and \(C\) is a parameter reflecting the inter-patch coupling strength. The functions \(f_i, g_i, h_i\) \((i = 1, 2)\) have the same form as in a single patch given by equation 1, with parameters \(a_i, b_i, c_i, x_{1i}, x_{2i}, \theta_i\) \((i = 1, 2)\). To start begin our analysis, we assumed that \(a_1 = a_2 = a, b_1 = b_2 = b, c_1 = c_2 = c, x_{11} = x_{12} = x_1, x_{21} = x_{22} = x_2, \theta_1 = \theta_2 = \theta\). Although considering identical parameters is not accurate from the ecological point of view, it provides a good test bed for investigations and serves as a useful starting point for analysing the coupled system. In this study we considered the parameter values \(a = 1, b = 1, c = 10, w^* = 0.006, x_1 = 0.5, x_2 = 1, k = 0.05\) (Blasius et al. 1999). We explored the dynamics of the coupled system under varying Allee parameter \(\theta\) and coupling strength \(C\), through numerical simulations using the Runge–Kutta fourth-order algorithm. We have corroborated the stability and convergence of our results with respect to decreasing step size.

3.1 Temporal evolution of population densities in coupled patches

Our first significant observation was the emergence of “blow-ups” in the vegetation population densities beyond a threshold of coupling strength. This threshold decreases with increase in the Allee parameter \(\theta\), namely, the onset of unbounded vegetation growth occurs at weaker coupling strengths for a stronger Allee effect. In order to quantify the advent of such blow-ups, we estimated the probability of unbounded vegetation growth from many initial states followed over an extended period of time, ensuring that the estimated values are converged with respect to the sample size of the initial conditions. In figure 1 we display the results thus obtained, for varying coupling strengths \(C\) and for values of the Allee parameter \(\theta = 0.001, 0.005\) and \(0.01\). It is clearly noticeable from the figure that for each value of the Allee parameter...
parameter $\theta$, there exists a critical value $C^*_0$ of coupling strength beyond which the vegetation has a non-zero probability of blow-up. It is also evident that for increasing values of $\theta$, the value of $C^*_0$ reduces. This clearly demonstrates that the Allee effect enhances the propensity of explosive vegetation growth, a trend that is consistent with the results from a single patch.

Note that a natural direction of future research would be to modify this model in order to achieve suppression of blow-ups. Proposals for modified models could include different approaches to ensure that the per-capita growth rate is finite at a low population density (Bazykin 1998). In another direction, mechanisms for the suppression of blow-ups could stem from varying the topology of the coupling connections (Choudhary et al. 2014). All these ideas provide interesting open avenues for future work.

Next, we looked into the temporal evolution of the population densities and the emergent attractors in phase phase of the coupled patches. To illustrate the dynamics of the coupled system, we present two representative time series and the corresponding phase space attractors in figure 2, for the Allee parameter $\theta$ equal to 0 (a–b) and 0.003 (c–d). The red dashed line corresponds to the mean $\mu$ of the time series and the black dashed line indicates the $\mu + 5 \sigma$ threshold.

Figure 2. Time series for the vegetation, prey and predator populations in a patch, and the corresponding phase space attractor of the system given by equations 2, for coupling strength $C = 0.1$, and the Allee parameter $\theta$ equal to 0 (a–b) and 0.003 (c–d). The red dashed line corresponds to the mean $\mu$ of the time series and the black dashed line indicates the $\mu + 5 \sigma$ threshold.
sufficiently large $\theta$. This phenomenon is demonstrated more rigorously through the bifurcation diagram in figure 3, which displays the emergence of chaos after a critical value of $\theta$. This trend is similar to that observed in a single patch. So, the influence of the Allee effect observed in a single patch generalizes to two coupled patches. Further, importantly, increasing the Allee effect parameter $\theta$ increases the size of the chaotic attractor in the coupled system. The sparse points at the high values of $u$, $v$ and $w$ are manifested as extreme events in the time series.

Figure 4 shows the bifurcation sequence with respect to coupling strength $C$, for $h = 0.003$ and $h = 0.003$. It has already been observed that in a single patch when the Allee effect is absent, all population densities evolve periodically with the system attracted to a period-4 orbit. However, interestingly, under coupling, even in the absence of the Allee effect, we observe that the populations in the patches evolve aperiodically when the coupling is sufficiently strong (see figure 4, top row). One also observes a periodic window arising near $C = 0.5$ in the bifurcation diagram as a result of an interior crisis.

The bifurcation diagrams for the case of the Allee parameter $\theta = 0.003$ are displayed in figure 4 (bottom row). The first significant observation is that chaos arises in the presence of the Allee effect, even in uncoupled patches. Further, we observe that increasing

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**Figure 3.** Bifurcation diagram of vegetation, prey and predator population densities (left to right), with respect to the Allee parameter $\theta$ for the coupling strength $C = 0.5$.

**Figure 4.** Bifurcation diagram of vegetation, prey and predator populations (left to right) in a patch with respect to the coupling strength $C$, for $\theta = 0$ (top row), and $\theta = 0.003$ (bottom row).
the coupling strength typically increases the size of the chaotic attractor, except in a small range $C \in [0.32, 0.411]$, where the system settles into a small period-2 attractor as a result of an interior crisis. This period-2 attractor once again becomes unstable as the coupling strength increases, giving rise to the sudden emergence of a large chaotic attractor. So, comparing the bifurcation scenarios for the two different cases, we can conclude that weak coupling induces chaos in the presence of the Allee effect, while for strong coupling, chaos arises even in the absence of the Allee effect.

Further, we explored the synchronization between the populations of vegetation, prey and predator in the two patches. In order to quantify the degree of synchronization we calculated the average synchronization error, defined as the mean square difference of the corresponding population densities of the two patches, obtained by averaging over long time and many initial states. It is clear that there is no synchronization, even for strong coupling. The closest synchronization (i.e. lowest synchronization error) is achieved in the parameter window supporting a period-2 orbit for $\theta = 0.003$, but typically the patches do not synchronize irrespective of the presence or absence of the Allee effect (figure 5).

3.2 Extreme events in the evolution of population densities

We first probed the global maximum of vegetation ($u_{\text{max}}$), prey ($v_{\text{max}}$) and predator ($w_{\text{max}}$) populations under increasing coupling strengths for different values of the Allee parameter $\theta$. We estimated $u_{\text{max}}$, $v_{\text{max}}$ and
$w_{\text{max}}$ by recording the maximum of the population of the patches from a large sample of random initial conditions. In figure 6 we plot $u_{\text{max}}$, $v_{\text{max}}$ and $w_{\text{max}}$ with respect to the coupling parameter $C$ for the Allee parameter $\theta = 0$ and $\theta = 0.003$. We observe that estimated values of $u_{\text{max}}$, $v_{\text{max}}$ and $w_{\text{max}}$ typically increase with rising coupling strength $C$, and this increase is more pronounced in the presence of the Allee effect. This shows that the Allee effect, as well as coupling strength, enhance the global maximum of the populations of all three species. This observation is consistent with the fact that increasing the Allee parameter and coupling strengths typically yields an increase in the size of the attractor in phase space, as evident from the bifurcation diagrams.

Next, we focused on the probability of obtaining extreme events for vegetation, prey and predator populations in the coupled patches in order to gauge the influence of the Allee effect and coupling strength on the advent of large deviations. With no loss of generality we considered the threshold of an extreme event to be $5\sigma$. In order to estimate the probability of obtaining extreme events, denoted as $P_{\text{ext}}$, we evolved the system from a large sample of random initial conditions over a prolonged time period and noted the occurrences when a population exceeded the $\mu + 5\sigma$ threshold. Figure 7 displays $P_{\text{ext}}$ for all three population densities with respect to the coupling strength for different $\theta$. In general, coupling enhances the occurrences of large deviations. Note, however, that when these deviations occur in periodic windows, such as near $C \sim 0.5$ for $\theta = 0$ and around $C \sim 0.3-0.4$ for $\theta = 0.003$, they are not true extreme events as they are entirely correlated in time and recur periodically.

When the Allee effect is absent (figure 7, left panel), the vegetation population is always confined to low values and does not show any extreme events. The prey population is, likewise, limited to small values for

**Figure 7.** Probability of obtaining extreme events in unit time in a patch ($P_{\text{ext}}$) with respect to coupling strength $C$, where $P_{\text{ext}}$ is estimated by sampling a time interval of length $T = 4000$ and averaging 1000 random initial conditions. We present this for two different values of the Allee parameter: (a) $\theta = 0$ and (b) $\theta = 0.003$. Here we considered that an extreme event occurs when a population exceeds the threshold value of $\mu + 5\sigma$. The case of vegetation is shown in blue, prey in red and predator in black.

**Figure 8.** Probability of obtaining extreme events in unit time in a patch ($P_{\text{ext}}$) with respect to the Allee parameter $\theta$. Here the coupling strength was fixed at $C = 0.25$, and $P_{\text{ext}}$ was estimated by sampling a time interval of length $T = 4000$ and averaging over 1000 random initial conditions. The case of vegetation is shown in blue, prey in red and predator in black.
lower coupling strengths. However, it deviates considerably from its mean beyond a critical threshold of coupling strength, resulting in extreme events. The predator populations have the highest propensity of extreme events, with extreme events arising even in uncoupled patches.

In the presence of the Allee effect (figure 7, right panel), one finds that both the predator and prey populations display large deviations from the mean, over the full coupling range, including the uncoupled case of $C = 0$. The only exception to this trend is the perceptible dip in extreme events around $C \sim 0.3 - 0.4$ for $\theta = 0.003$, corresponding to a period-2 orbit (cf. figure 4, lower panels). The most significant result in the coupled patches in the presence of the Allee effect is the emergence of a small finite probability of extreme events in the vegetation population for sufficiently strong coupling.

These trends are further borne out by figure 8, which displays $P_{\text{ext}}$ over a range of Allee parameters for a fixed value of coupling strength. It is again apparent that predator populations exhibit the highest propensity for large deviations from the mean, and this is not affected much by the magnitude of the Allee effect. The prey population, on the other hand, shows a steady increase in extreme events with increasing Allee parameter. However, $P_{\text{ext}}$ for the prey is always lower than that for predators. The vegetation shows no extreme events at this value of coupling strength, even when the Allee effect is present.

An interesting and open direction of investigation is to explore the commonalities and differences of the phenomena observed here by comparing them with those arising in diffusively coupled patches. The interplay of the strength of diffusive coupling and the Allee effect is expected to induce new phenomena. Our preliminary results from diffusively coupled patches show that in the ranges of Allee parameters and coupling strengths where the populations are non-extinct and bounded, extreme events occur. However, the quantification of the frequency of these events, and the robustness of this observation under varying model parameters, are still open and important problems.

3.3 Effect of noise on extreme events

Noise is prevalent in natural ecosystems as a result of external factors such as inherent diversity, fluctuations in migration, and environmental changes. Here we examined how stochasticity influences the three-species coupled system (equation 2). Specifically, we explored the dynamics of the system under additive random noise $\xi(t)$, given by the following dynamical equations:

\begin{align}
\dot{u}_1 &= f(u_1, v_1, w_1) + \xi_1(t), \\
\dot{v}_1 &= g(u_1, v_1, w_1) - C v_1 w_2 + \xi_2(t), \\
\dot{w}_1 &= h(u_1, v_1, w_1) + C v_2 w_1 + \xi_3(t), \\
\dot{u}_2 &= f(u_2, v_2, w_2) + \xi_4(t), \\
\dot{v}_2 &= g(u_2, v_2, w_2) - C v_2 w_1 + \xi_5(t), \\
\dot{w}_2 &= h(u_2, v_2, w_2) + C v_1 w_2 + \xi_6(t)
\end{align}

The functional forms $f(u, v, w)$, $g(u, v, w)$ and $h(u, v, w)$ are given as before in equation 1, and $\xi_i(t)$, $i = 1, 2, \ldots, 6$, represents zero mean delta-correlated Gaussian white noises satisfying $<\xi_i(t), \xi_j(t')> = \sigma \delta(t - t') \delta_{ij}$ for $i, j = 1, 2, \ldots, 6$, where $\sigma$ is the noise strength. Note that in this work we considered all the state variables to have similar magnitudes of noise. Naturally different noise strengths may be relevant for different variables, and this is an avenue open for interesting exploration.

In our work, in order to explore the dynamics of the coupled system in the presence of additive noise, we investigated the dynamics of the stochastic differential system (equation 3) numerically by using the explicit Euler–Maruyama scheme. We have also checked the convergence and stability of the numerical solutions with decreasing step size. In particular, we explored whether the system becomes more irregular, or if chaos is suppressed to noisy cycles or noisy fixed points, in the presence of stochasticity. In figure 9 we present the time series and phase portrait of the system (equation 3) for different noise strengths. It is observed that when noise strength is either zero or of very low magnitude ($\sigma = 10^{-3}$), all three populations oscillate aperiodically and the system evolves to chaotic attractors (figure 9a–b). Also note that populations of all species exhibit extreme events for low magnitude of noise strength as their states occasionally cross the $\mu + \ldots$
5σ threshold. On increasing noise strengths (σ ~ 5 × 10^{-3}), these extreme events completely disappear from the all populations, and the populations of all three species settle into a noisy periodic orbit (figure 9c–d). On further increasing the noise strength (σ ~ 10^{-2}), the populations of all three species settle down to a noisy quasi-steady state (figure 9e–f), and the system continues to exhibit no extreme deviations from the mean. So, then, very interestingly, the extreme events in the populations of this coupled three-species system are suppressed under sufficiently strong noise. Therefore, we arrived at the following significant conclusion: additive noise not only suppresses the extreme events in the vegetation, prey and predator populations, but it also transforms the dynamics of the system from chaos to a noisy quasi-steady state. Also, additive noise tames the explosive growth in the vegetation population that we had observed earlier.

4. Discussion

In summary, we explored the dynamics of two coupled patches of a three-species trophic system by incorporating the Allee effect in the prey population. Our focus was on the emergence of extreme events in the system. In particular, we addressed the significant question of whether or not the Allee effect and coupling suppress or enhance extreme events. Our first key observation was as follows: we found that the system experiences an explosive blow-up in the vegetation population after a critical value of coupling strength in the presence of the Allee effect. Further, the interplay of the Allee effect and coupling has a pronounced influence on the nature of the dynamics. In order to explore this aspect in detail, we looked into the bifurcation scenarios of the system with respect to the Allee parameter θ and coupling strength C. We found that the populations of all three species of the coupled system (equation 2) oscillate in a regular manner and settle into a period-4 orbit when the Allee parameter θ is low, whereas the populations fluctuate aperiodically and chaotic attractors emerge in the coupled system with increase in the Allee parameter θ. In addition, the size of the attractor gradually increases with the increasing Allee parameter θ, which is compatible with trends from a single patch. It was also clearly evident that coupling induces chaotic behaviour in the system. Further, interspersed in the chaotic regimes one finds periodic windows that arise from an interior crisis in certain ranges of coupling strengths. The notable difference stemming from the Allee effect is that there is chaos for low coupling strengths, including the case of C = 0 (i.e. the uncoupled case) for finite θ, while weakly coupled patches with no Allee effect exhibit regular dynamics.

Most importantly, we observed that for large enough coupling strengths and Allee parameters, all population densities exhibit a non-zero probability of yielding extreme events. In general, the predators have the largest propensity for extreme events in coupled patches, and the vegetation population densities exhibit the least number of extreme occurrences. Further, the emergence of extreme events in the predator population is not affected much by either the coupling strength or the Allee effect. For prey populations, in the absence of the Allee effect, there are no extreme events for low coupling strengths, but there is a sharp increase in extreme events after a critical value of the coupling strength. For the vegetation population, a small finite probability of extreme events emerges for strong enough coupling, only in the presence of the Allee effect.

Lastly, we considered the influence of additive noise on extreme events. We found that noise tames the unbounded vegetation growth induced by the coupling and the Allee effect. More interestingly, we demonstrated that stochasticity drastically diminishes the probability of extreme events in all three populations in the coupled patches. In fact, for sufficiently high noise, we did not observe any more extreme events in the system. This indicates that noise can mitigate extreme events, and potentially has an important impact on the observability of extreme events in naturally occurring systems.

Acknowledgements

This paper is in honour of Professor Somdatta Sinha, who continues to inspire us to use mathematical formalisms to understand wide-ranging problems arising in biological contexts.

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Corresponding editor: MOHIT KUMAR JOLLY